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Studies in the genus *Hypericum* L. (Guttiferae) 4(1). Sections 7. *Roscyna* to 9. *Hypericum* sensu lato (part 1)

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CONTENTS

SYNOPSIS. Following the removal of *Hypericum ellipticifolium* H.L. Li to a new genus, *Lianthus* N. Robson **gen. nov.**, which is described, the variation, distribution and evolution of *Hypericum* sects 7–9 (all herbaceous) are discussed. It is shown that, whereas sect. 7. *Roscyna* is indeed derived from sect. 3 *Ascyreia* (as was indicated in Parts 1–3), sect. 8. *Bupleuroides* is not directly related to sect. 7 but to the Chinese suffrutex *H. elatoides* R. Keller, which, in turn, is shown to belong to sect. *Ascyreia*, not sect. *Roscyna*. Sect. 9. *Hypericum* is considered to be a complex of six sections each derived directly from sect. *Roscyna*, of which one (sect. 9a. *Concinna* N. Robson) has already been described. The others are: sect. 9 *Hypericum* (which is divided into two subsections: 9.1 *Hypericum* and 9.2 *Erecta* N. Robson, **subsect. nov.**, with subsect. *Hypericum* further divided into two series, *Hypericum* and *Senanensia* N. Robson, **series nov.**), 9b. *Graveolentia* N. Robson, **sect. nov.**, 9c. *Sampsonia* N. Robson, **sect. nov.**, 9d. *Elodeoida* N. Robson, **sect. nov.** and 9e. *Monanthema*, **sect. nov.** A systematic treatment is then provided of *H. elatoides* and sects *Roscyna*, *Bupleuroides*, *Concinna*, *Sampsonia*, *Elodeoida* and *Monanthema*.

INTRODUCTION

Part 4 of the *Hypericum* monograph includes treatments of those sections derived directly or indirectly from sect. 3. *Ascyreia* in the affinity of the Nepali endemic *H. podocarpoides* N. Robson (see Part 3, Robson, 1985: 170, fig. 4). Part 4(1) provides an introduction to the whole group and systematic treatments of sect. 7 and part of sect. 9. Also treated are *H. bupleuroides* Griseb., in the monotypic sect. 8 *Bupleuroides*, and *H. elatoides* R. Keller (its nearest relative in sect. 3. *Ascyreia*), which was wrongly included in sect. 7. *Roscyna* in Part 1 (Robson, 1977). The opportunity has also been taken to remove *H. ellipticifolium* H.L. Li to a new genus; by implication it has hitherto been included in the rather amorphous sect. 9. *Hypericum*.

Before turning to these taxa, however, it is desirable to draw attention to two potentially misleading errors that crept into Part 6:

(1) On p. 121, the record of 2n = 16 chromosomes by Löve & Löve refers to *H. majus* (A. Gray) Britton (sect. *Trigynobrathys*), not to *H. ellipticum* Hook. (sect. *Myriandra*). All records for the latter section, therefore, are n = 9 or 2n = 18.

(2) On p. 180, the record for *H. aethiopicum* subsp. *sonderi* in the middle of Namibia (Map 32) is an error, as reference to the text will show. The dot became displaced from among the south-east African records during printing.

Finally, as it has not been possible to continue producing the distribution maps by hand, they have been made on computer. However, this has necessitated the omission of co-ordinates and Chinese provincial boundaries. Text figures of leaf, petal and diagrammatic inflorescence for each species have also, unfortunately, had to be omitted because of time constraints.

Further delimitation of *Hypericum* – exclusion of *H. ellipticifolium* H.L. Li

Hui-lin Li's (1944) description of a suffruticose *Hypericum* with white flowers (from the border of Yunnan and Myanmar) indicated the need for further investigation. An examination of the type and other specimens revealed that, as suspected, the flower had three very small fasciclodes inserted between the stamen fascicles, i.e. that the affinities of this species were with *Triadenum*, not *Hypericum*. In fact it appears to be basic to the *Triadenum-Thornea* group, which, in Parts 1 (Robson, 1977: 300) and 2 (Robson, 1981: 63), I placed with *Eliea* and *Cratoxylum* in the Hypericoideae–Cratoxyleae. However, following the discovery by Gibson (1980) that the secondary xylem of *Thornea*, *Triadenum* and *Hypericum* is organised on a common design that is quite different from that of the *Cratoxyleae*, I re-examined the problem and now agree with him and with Stevens (in press) that the *Triadenum* group is most closely related to *Santomasia* and *Hypericum* but forms a clade in the Hypericeae distinct from them.

Lianthus N. Robson, **gen. nov.**

Triadeno Rafin. affine, a quo habito suffruticoso, foliis canaliculis et glandulosis pellucidis continentibus, petalis albis, staminibus plurimus, differt.

Suffrutex, glabrous, without black glands, with stems caespitose or shortly rhizomatous, slender. *Stems* and branches terete, eglandular. *Leaves* opposite, entire, exstipulate, venation pinnate, dorsal, with translucent ('pale') glands only; glands in 2 systems: (1) dorsal – punctiform, (2) ventral – closely parallel, linear or ± interrupted, arching from near base. *Inflorescence* terminal, few-flowered, cymose, umbelliform. *Flowers* bisexual, homostylous. *Sepals* 5, quincuncial, persistent. *Petals* 5, white, subsymmetric, apiculate, deciduous. *Stamen fascicles* '3' (i.e. 2 + 2 + 1), with filaments in each fascicle united at the base, deciduous, the stamens totalling 11–15; fasciclodes 3, very small, inserted between stamen fascicles, persistent. *Ovary* 3-locular with loculi many-ovulate; styles 3, free, elongate, slender; stigmas narrowly capitate. *Fruit* capsular, septicidal, with valves longitudinally and narrowly vittate. *Seeds* numerous, small, fusiform, carinate, with testa finely foveolate; embryo not examined. *Pollen grains* not examined.

TYPUS GENERIS. *L. ellipticifolius* (H.L. Li) N. Robson.

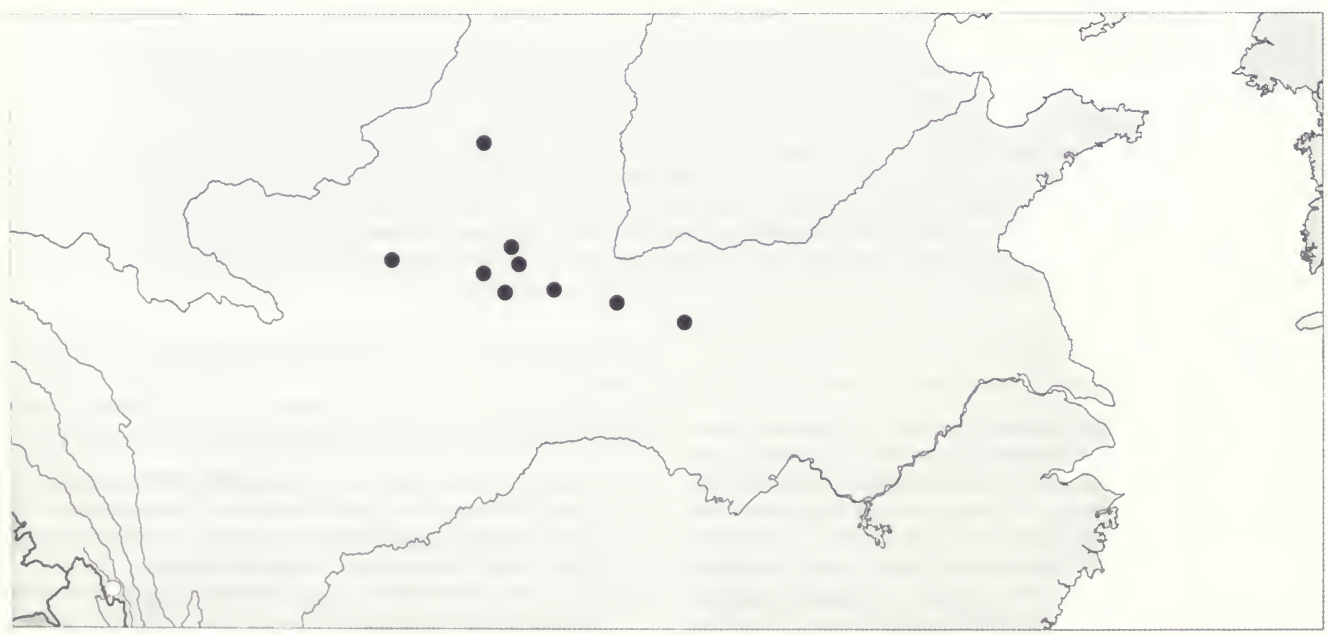
Genus adhuc monospecificum.

Lianthus ellipticifolius (H.L. Li) N. Robson, **comb. nov.** Type as for *Hypericum ellipticifolium* H.L. Li.
Fig. 1, Map 1.

Hypericum ellipticifolium H.L. Li in *J. Arnold Arbor.* **25**: 307 (1944); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 8, t. 1 ff. 5–6 (1990). Type: China, Yunnan, Taron-Taru divide, valley of Bucahwang, 2200 m, 4 September 1938 (fl & fr), *T.T. Yü* 20125 (A!-holotype; KUN!-isotype).

Icon: Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 8, t. 1 ff.. 5–6 (1990).

Suffrutex 0.3–0.6 m tall, erect, caespitose or from shortly creeping and rooting base, with stems few. slender, sometimes branched above. *Stems* terete, eglandular; internodes 30–45 mm, equalling or usually exceeding leaves. *Leaves* sessile; lamina 30–50 × 15–30 mm, elliptic, paler beneath, not glaucous, chartaceous; apex rounded to subretuse, often obtusely apiculate, margin entire, base rounded; venation: 2–3(4) pairs of main laterals from lower third of midrib, with tertiary reticulation lax, only main veins visible (and prominent) below; laminar glands (dorsal) very small, irregular, dense; laminar glands (ventral) linear, curved-parallel from base and sometimes crossing veins, alternating with vein-like narrower, distally interrupted glands; marginal glands rather dense. *Inflorescence* 5–7-flowered, subumbelliform, from terminal node only; pedicels



Map 1 *Lianthus ellipticifolius* ○; *Hypericum* sect. 3: 16a. *H. elatoides* ●.

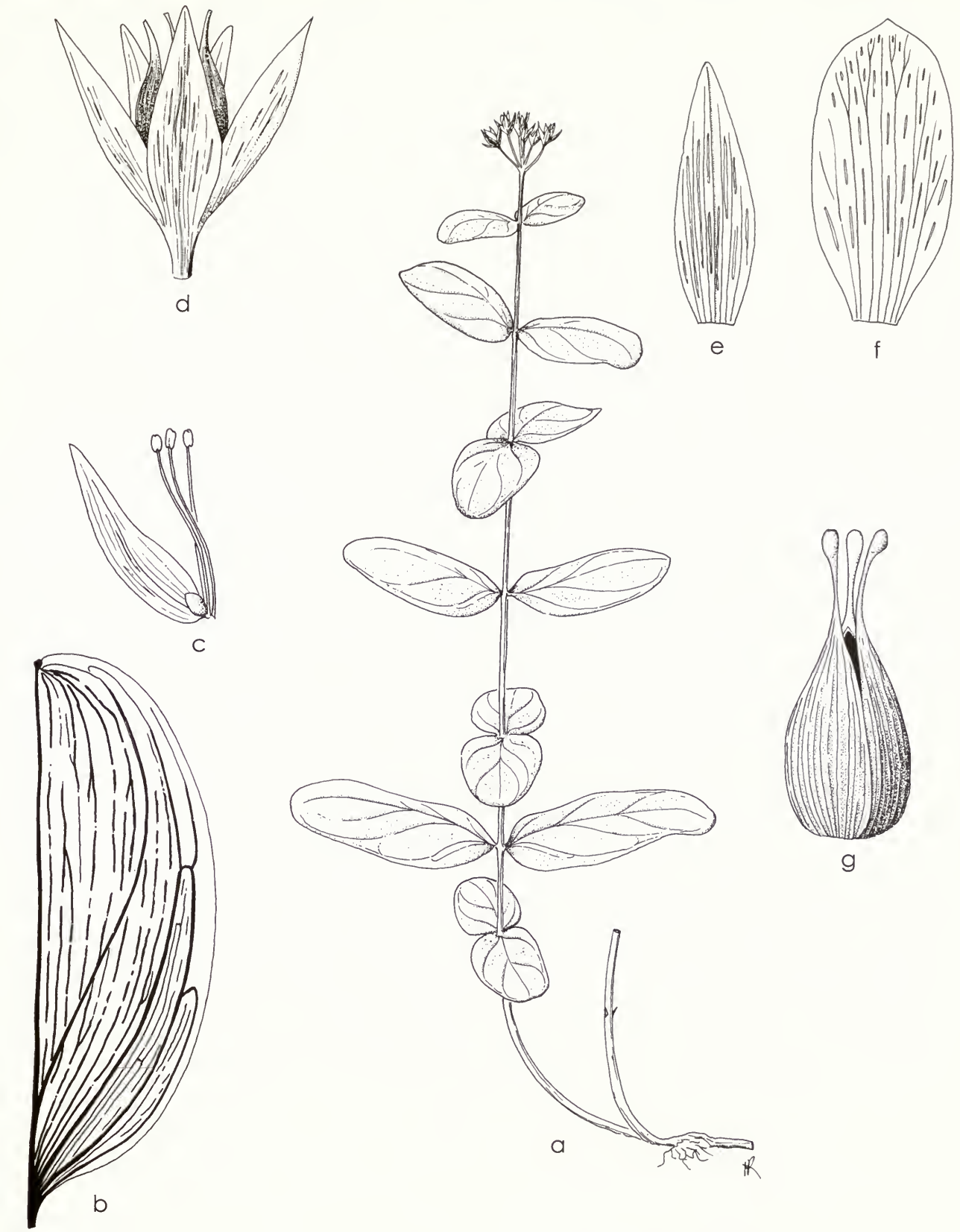


Fig. 1 *Lianthus ellipticifolius*: (a) habit; (b) half leaf, showing primary and secondary venation, with tertiary venation (below) and venation system crossing veins (above); (c) sepal with fasciclode and 3-stamened fascicle; (d) flower with fruiting capsule; (e) sepal; (f) petal; (g) capsule beginning to dehisce (a × 2/3, b × 2, c–g × 6). (a) *T.T. Yü* 20868, except base; (a) base and (b)–(g) *T.T. Yü* 20125.

c. 8 mm; bracts 1–1.5 mm long, narrowly triangular. *Flowers c.* 15 mm in diam., stellate?; buds elliptic, obtuse. *Sepals* equal, 6–7 × 2 mm, erect in bud, reflexed in fruit, narrowly triangular-lanceolate, narrowly acute to acuminate, entire; veins 5, outer sometimes branched; laminar glands linear, usually 2 between each vein; marginal glands absent. *Petals* white, 10–12 × 3–4 mm, *c.* 2 × sepals, oblong-obovate, entire, with apiculus lateral, very short; laminar glands linear to striiform; marginal glands absent. *Stamens c.* 11–15, '3'-fascicled (6 + 5 + 4? to 5 + 3 + 3), 8–9 mm, *c.* 0.75 × petals; anther gland amber. *Fasciclodes* 3, very small, lenticular. *Ovary* 3-locular, *c.* 5 × mm, ovoid; styles 3, *c.* 2 mm, *c.* 0.4 × ovary. *Capsule* 7 × 4 mm, about equalling sepals, ovoid; valves narrowly vittate. *Seeds* dark brown, *c.* 0.6 mm, fusiform, acuminate at extremities, carinate; testa finely foveolate.

Grassy slopes; 1800–2200 m.

China (Yunnan).

CHINA. Yunnan: Taron-Taru Divide, Tangtehwang to Bucahwang, 1800 m, 29 October 1938 (fl & fr), *T.T. Yü* 20868 (IBSC, KUN); west of Dulongjiang, 1800 m, 17 November 1959 (fl), *G.M. Feng* 24299 (KUN). See also type.

Lianthus is named primarily after Hui-lin Li, who described its sole species as a *Hypericum*, but this name also commemorates Li Xiwen, who has published helpful accounts of *Hypericum* and *Triadenum* for several Chinese Floras. It differs from *Hypericum* in several respects, e.g. in having white petals and fasciclodes and, most notably, in its two systems of foliar glands. Viewed from above, the leaf has venation and pale punctiform glands similar to those of *Triadenum* and many *Hypericum* species. From below, however, although the main venation system is visible (indeed prominent), it is crossed by what appears to be another venation system of numerous parallel veins interspersed with linear glands.[1]

These 'veins' and glands form two arching groups originating at or near the base of the leaf and each following the curve of the adjacent leaf margin. On closer inspection, the 'veins' in this system, which have cross-connections and λ junctions similar to a normal primitive venation system (see Melville, 1976), appear to be secretory, not true veins; and so the whole system is a 'fossil' venation that seems to have been replaced functionally by the dorsal veins described above. This situation is known elsewhere in the Guttiferae, especially in the Clusioideae (e.g. *Garcinia* – Robson, 1961; Jones, 1980), and in the Thymelaeaceae (Melville, 1983); and the transition from one system to the other is noticeable in the most primitive taxa of *Hypericum* (*H. bequaertii* De Wild. and *H. revolutum* subsp. *keniense* (Schweinf.) N. Robson), see Robson (1981: 80).

With this suite of foliar differences, together with the floral differences already mentioned, it is clear that *Lianthus* cannot be derived from any species of *Hypericum*. Its immediate relationships are with *Triadenum* and *Thornea*, genera which I now place in the Hypericoideae–Hypericeae (see above). They form a group in that tribe distinct from *Santomasia* and *Hypericum*. This group apparently lacks the yellow flavonoid that normally occurs in the petals of *Hypericum*, and therefore their petals are white to red (white in *Lianthus*, white or pink to carmine in *Triadenum*, pink or white and pink in *Thornea*); they have few (3–5) stamens in each of three fascicles, so that the 'double' antesepalous fascicles have fewer than double the number of stamens of the single antepetalous one, often the same number. The range of chromosome numbers in *Triadenum* is now known to include 2n = 36 (Probatova & Sokolovskaya, 1983, 1986) as well as 2n = 38 (n = 19, Hoar & Haertl, 1932). In relation to *Hypericum*, where the original base number appears to be x = 12, the numbers in *Triadenum* would seem to be part of a tetraploid reduction series based on n = 10, i.e. 2n = 40. On the other hand, the morphologically more primitive *T. japonicum* (Blume) Makino has 2n = 36 whereas *T. virginicum* (L.) Rafin. has 2n = 38, and so the series could be an ascending one.

In terms of geographical and evolutionary trends, the *Triadenum* group fits together well. *Lianthus*, a suffrutex with a terminal inflorescence, 11–15 stamens, and sessile leaves with the remains of an ancient venation system, is confined to a very small area in western Yunnan near the Myanmar border. *Triadenum*, marsh herbs with terminal and axillary flowers or partial inflorescences, 9 stamens, and sessile to petiolate leaves with only the 'recent' vascular and gland system, has one species in Assam and south China, one in Japan, Korea and adjacent Siberia and China, and four in eastern North America, all in lowland areas. *Thornea*, evergreen shrubs with inflorescences terminal and terminating lateral branches, 9 stamens, and petiolate leaves with only the 'recent' vascular and gland system (and the smallest flowers in the group), has one species in southern Mexico (Chiapas) and Nicaragua (Jinotega) and a second (more reduced) in Mexico (Chiapas) and Guatemala (Huehuetenango), both in montane habitats. The group would therefore seem to have spread from south China northward, across the Bering Bridge and southward through North America to Nicaragua, the southern Asian species of *Triadenum* (*T. brevifolium* (Wall. ex Dyer) Y. Kimura) being a development from the northern *T. japonicum*. From this view, the shrubby habit of *Thornea* appears to be the result of an evolutionary reversion, but, since the genus in all other characters is advanced in relation to *Triadenum*, I cannot see a satisfactory alternative hypothesis.

Relationship of *H. elatoides* and sect. 8. *Bupleuroides* (Fig. 2)

Although Keller had described *H. elatoides* in 1904, placing it in sect. *Norysca* (i.e. sect. 3. *Ascyreia*), he omitted it from the 2nd edition of *Die natürlichen Pflanzenfamilien* (Keller, 1925). On the basis of the limited material available to me when working on Part 1, I decided that the petals and stamens were persistent and the habit herbaceous, characters that led me to place this species in sect. 7. *Roscyna* (Robson, 1977). Subsequent examination of more abundant material has revealed that the petals and stamens are tardily deciduous and the habit suffruticose. Keller was therefore correct; *H. elatoides* belongs to sect. 3. *Ascyreia* and appears to be a derivative of the variable *H. monogynum* L. The tardily deciduous petals and stamens, the large leaves, often cordate-amplexicaul at the base, and the sometimes minutely reddish-glandular-ciliate sepal margin all indicate a trend to the monospecific sect. 8. *Bupleuroides*, where the stamen fascicles are '3' and the ovary trimerous, the petals and stamens are persistent, the leaves are perfoliate, and the sepals are sometimes minutely reddish- to black-glandular-ciliate. The distributional gap between north-west China and the south-east Pontic region is paralleled by that between the areas of another part of *H. monogynum* and the monospecific sect. 6. *Inodora* (see Robson, 1985: 314). It is thus necessary to add *H. elatoides* to sect. 3. *Ascyreia* as Species 16a, which can be inserted in the key (Robson, 1985: 207) as follows:

20(16) Leaves densely reticulate-veined beneath, (20–)30–110 mm long; inflorescence 1–30-flowered, terminal on long shoots 20a

Leaves without visible reticulate venation beneath, 10–31 mm long; inflorescence always 1-flowered, terminal on long and on short lateral shoots ..... 19. **longistylum**

[1]Lü & Hu (unpublished) provide support for the generic separation of *H. ellipticifolium* from a study of epidermal micro-morphology in *Hypericum* and *Triadenum*.

20a(20) Petals and stamens tardily deciduous; sepal margin sometimes minutely reddish-glandular-ciliate; plant a suffrutex .... 16a. **elatoides**

Petals and stamens soon deciduous; sepal margin entire; plant a shrub 21

21(20a) Leaves with base cuneate to rounded, or if cordate then apex rounded; leaf lamina usually broader at or above middle .... 16. **monogynum**

Leaves with base cordate-amplexicaul, apex acute to acuminate; leaf lamina elliptic-ovate to broadly ovate ..... 18. **prattii**

Relationships of sects 7. *Roscyna* and 9. *Hypericum* sensu lato (Fig. 2)

With the removal of *Hypericum elatoides* to sect. *Ascyreia*, sect. *Roscyna* consists of two variable herbaceous species with regular pentamerous flowers and persistent petals and stamens: *H. ascyron* L. and *H. przewalskii* Maxim. *H. pedunculatum* R. Keller, which was included with a query in Part 1, cannot be distinguished from *H. przewalskii*. It is the nearest form of that species morphologically to *H. ascyron*.

H. ascyron is distributed from the Altai region and adjacent Xinjiang through southern Siberia to Kamchatka and south to Japan, China (except Xizang and Qinghai), Taiwan and Vietnam, and also in eastern North America. It can be divided into three subspecies: (i) subsp. *ascyron* (Siberia from Ob and Altai eastward to Ussuri, Japan, Korea, China, Vietnam, Taiwan), (ii) subsp. *gebleri* (Ledeb.) N. Robson (Xinjiang, upper Altai region, montane and far-eastern parts of Siberia, northern Mongolia, northern China, Sakhalin, northern Kurile Is. and Kamchatka), (iii) subsp. *pyramidatum* (Aiton) N. Robson (eastern North America). Subsp. *ascyron* (the morphologically primitive taxon), having apparently given rise to the other two subspecies, is most closely related to *H. podocarpoides* (sect. 3. *Ascyreia*), endemic to central Nepal. The whole of the Himalayan massif and Tibetan Plateau thus separates the ranges of these species.

H. przewalskii, which occurs in western China from Qinghai and Gansu south to Yunnan, differs from *H. ascyron* in its usually 2-lined to terete stem internodes and usually broader leaves with obtuse to retuse apex. '*H. pedunculatum*' is a narrow-leaved much-branched form of *H. przewalskii* from western Hubei that is linked to the more typical unbranched broad-leaved form by intermediates.

With virtually no intermediate forms between the regular pentamery of the floral whorls of sect. *Roscyna* and the trimery and pseudotrimery of the inner whorls in sect. *Hypericum* sensu lato (apart from one or two aberrant cases of tetramery in the gynoecium (and androecium?), e.g. *H. kelleri* H. Léveillé (=*H. ascyron*) and *H. paradoxum* R. Keller (=*H. kamtschaticum*)), previous authors (e.g. Keller, 1925) have placed nearly all herbaceous species with trimerous inner floral whorls in a large section *Hypericum* or *Euhypericum*. The absence of black glands from sect. *Roscyna* species and their invariable presence at least somewhere in those of sect. *Hypericum* seemed to confirm their classification. We have already seen, however, that this unwieldy 'section' contains three distantly related groups – sects 9, 10–19 and 27 (Robson, 1977, 1996). It is perhaps, therefore, not surprising that sect. 9. *Hypericum* itself can be broken down further into sections and subsections.

Dismemberment of sect. 9. *Hypericum*

Sect. 9. *Hypericum* has been shown to comprise seven recognizable taxa. Although they are all related to species in sect. 7. *Roscyna*, six of them are not directly related to one another; so they have been treated as sections and the two interrelated ones as subsections (Figs 2–4).

(i) The north Californian endemic *H. concinnum* Benth. has already been removed from sect. 9 to its own section, sect. 9a. *Concinna* N. Robson (Robson, 1981: 173), on the basis of its narrow concolorous, often conduplicate leaves, large sepals and amber anther gland. The only part of sect. *Roscyna* that approaches it morphologically is *H. ascyron* subsp. *gebleri*, in which the leaves are sometimes very narrow ('*H. sachalinense* H. Léveillé') and the sepals are not very different from the narrowly to broadly ovate ones of *H. concinnum*. In addition,

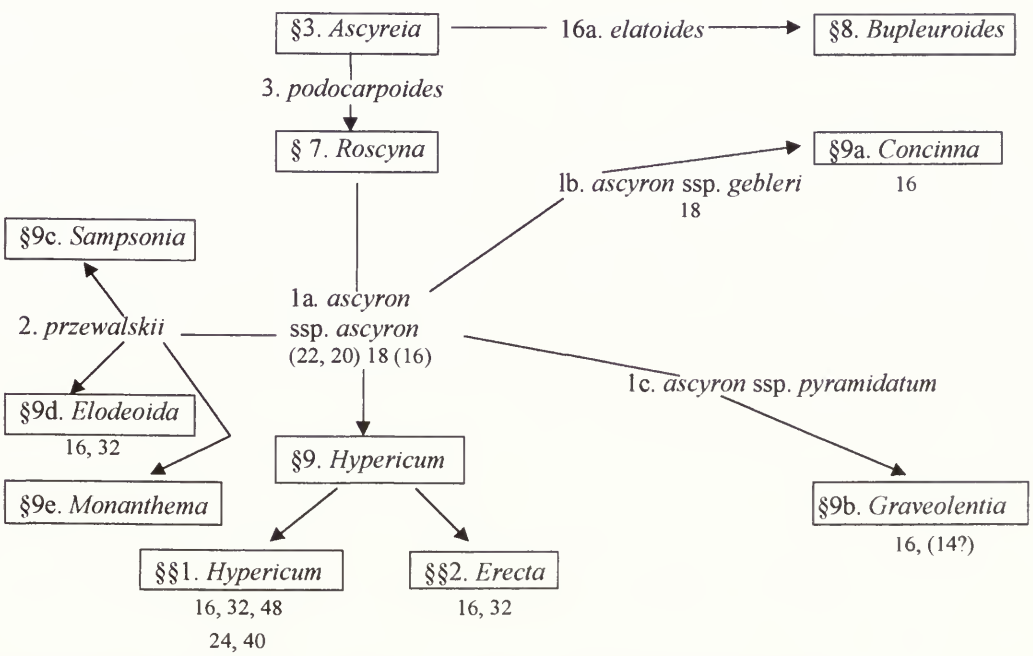


Fig. 2 Sections 7–9e. Relationships and chromosome numbers (2n), indicating derivations from sect. 3 *Ascyreia*.

the presence of subsp. *gebleri* in Kamchatka and the northern Kurile Is. suggests that it or its derivative could well have crossed over to North America.

(ii) The other North American group belonging to sect. *Hypericum* occurs in the east, in extreme southern Canada, the U.S.A., eastern and southern Mexico and Guatemala. As this group proved difficult initially to separate from the Japanese species of this section, another trans-Pacific distribution appeared to be involved. Such a hypothesis turned out to be unnecessary, however, when the stem glandular patterns were compared. Furthermore, the acute sepals with linear laminar glands and the 4-lined young stem internodes of the most primitive species (*H. graveolens* Buckley) could have been derived only from the North American subspecies of *H. ascyron*, subsp. *pyramidatum*. The anther gland is exceptionally amber in one species, *H. pseudomaculatum* Bush. This group has thus been given sectional rank as sect. 9b. *Graveolentia* **sect. nov**.

The five remaining groups can be divided into those that can be derived directly from *H. ascyron* subsp. *ascyron* (with stem internodes basically 4-lined) and those most closely related to *H. przewalskii* (with stem internodes basically terete).

(iii) The basically 4-stem-lined group comprises one subgroup (iiia) in which the rootstock is herbaceous and stoloniferous and 2 or 4 stem-lines are always present, at least when young, and usually bear at least some dark glands, and another subgroup (iiib) with a woody or fibrous rootstock and eventually terete stems, from which stem-line glands are always absent. Since group (iii) contains the generic type, *H. perforatum* L., it remains as sect. 9. *Hypericum* and subgroup (iiia) becomes subsect. 1. *Hypericum*.

Subgroup (iiia) (i.e. subsect. *Hypericum*) comprises two subgroups with distinct distributions (a: Eurosiberia, and also Japan, and western North America; b: north Japan, Korea and central China), which have as respective basic taxa the Balkan *H. maculatum* subsp. *immaculatum* (Murb.) A. Fröhl. and the northern Japanese *H. kamtchaticum* var. *pibairense* Miyabe & Y. Kimura, taxa that resemble one another closely. Subgroup (a) in turn has two centres of distribution (Europe–western Siberia and eastern Siberia–western North America), the parts of which are now linked by the Asiatic distribution of *H. perforatum*, a presumed hybrid with one parent in each part, and *H. elegans* Stephan ex Willd., an eastern species that has spread westward from central Asia into Europe. The species of subgroup (b) lack black glands on the stem-lines, which eventually disappear in growth, whereas black-gland-bearing stem-lines are all but constant in subgroup (a). These two subgroups can thus be distinguished respectively as (iiiaa) series 1. *Hypericum* and (iiiab) series 2. *Senanensia* **series nov.**

The other main subgroup (iiib) contains the widespread and variable *H. erectum* Thunb. and has been named subsect. 2. *Erecta* **subsect. nov.** Stem lines are present only in the primitive taxa (e.g. *H. yamamotoi* var. *riparium* Y. Kimura) and, even then, rarely persist into maturity; the stems never bear dark glands except in *H. nikkoense* Makino, which sometimes has scattered black or reddish ones. Its distribution is centred in northern Japan, extending into the rest of Japan and adjacent areas of the Russian Federation, Korea and China as well as Taiwan, the Philippines and Borneo.

(iv), (v) and (vi) Three groups are derived morphologically from *H. przewalskii* but appear to be related to different parts of this variable species. Although all have terete eglandular mature stem internodes (except sometimes when the stem is very slender, when they may be 2–6-lined and, in one species, rarely with some reddish glands on the lines), they are otherwise quite different.

(iv) *H. sampsonii* Hance has a wide distribution in east Asia from southern Japan and Taiwan to central Myanmar; and a clearly derived species, *H. assamicum* Biswas, extends the area of this group to Assam (Meghalaya). These plants have leaves like those of '*H. pedunculatum*', but they are perfoliate and broader at the point of union. The inflorescence, however, is multifloral, the flowers are much smaller with a subcupuliform base, and the three capsule valves bear elongate to punctiform amber vesicular glands. Taken together, these characters are quite diagnostic and indicate that these two species merit segregation into a separate section, 9c. *Sampsonia* **sect. nov.** The perfoliate leaves of *H. bupleuroides* and the sometimes vesicular capsule valves of *H. perforatum* are parts of quite different character syndromes. There is no evidence supporting Kimura's (1951) allocation of *H. sampsonii* to the mainly Balkan-Mediterranean sect. 13. *Drosocarpium* on account of the vesicular capsule valves.

(v) Another group of species related to *H. przewalskii* is linked to the narrow-leaved branching form, '*H. pedunculatum*', through its most primitive species, *H. seniawinii* Maxim. In addition to the trimery of the inner floral whorls and the intramarginal foliar black glands, *H. seniawinii* differs from '*H. pedunculatum*' in having acute sepals with marginal black glands. It resembles the latter, however, in its relatively large and dense laminar leaf glands. Other species in this group have black-glandular fringes to auriculate appendages of the leaves or sometimes of the leaf itself. The distribution of the group extends from east and south China to north Vietnam, thence westward along the Himalaya to Kashmir. The section has been named after the widespread *H. elodeoides* Choisy, sect. 9d. *Elodeoida* **sect. nov.**

(vi) The final group is related to the few-flowered broad-leaved form of *H. przewalskii* that occurs in Sichuan and adjacent Yunnan ('*H. macrosepalum*'). Like it, this group of species has small laminar leaf glands that are usually sparse and may be almost absent, and its primitive species have similar broad leaves. Its distribution extends from south and south-west China through north Laos, north Thailand and north Myanmar along the Himalayan range to Pakistan, and it also occurs in south India and Sri Lanka. The section has been named after the widespread *H. monanthemum* Hook. f. & Thoms. ex Dyer, sect. 9e. *Monanthema* **sect. nov.**

The subdivision of sect. 9. *Hypericum* sensu lato can be summarised as follows:

Sect. 9. *Hypericum*. Mature stem internodes 2–4-lined or terete; dark glands, when present, nearly always confined to lines. Leaves free, entire, exappendiculate, plane to marginally recurved; laminar glands dense to sparse or absent. Bracteoles entire or very rarely glandular-denticulate (*H. elegans*), reduced. Flowers stellate. Perianth 5-merous. Sepal laminar glands nearly always striiform to punctiform. Anther gland black. Capsule valves longitudinally vittate or rarely obliquely vittate to vesiculate, vesicles amber. 42 species.

Subsect. 1. *Hypericum* (Part 4(2,3)). Rootstock herbaceous, stoloniferous. Mature stem internodes usually persistently 2–4-lined; dark glands usually present, nearly always confined to lines. Capsule valves nearly always longitudinally vittate, occasionally interrupted or with oblique swollen lateral vittae or vesicles. 19 species.

Series 1. *Hypericum* (Part 4(2)). Stems persistently lined; lines prominent (except in 12. *H. scouleri* Hook.), sometimes almost winged, bearing dark glands (sometimes except 12. *H. scouleri*). 12 species.

Series 2. *Senanensia* (Part 4(3). Stems becoming terete; lines weak, eglandular. 7 species.

Subsect. 2. *Erecta* (Part 4(3)). Rootstock woody to fibrous, not stoloniferous. Mature stem internodes slightly 2(4)-lined or usually terete; dark glands nearly always absent, when present not on lines. Capsule valves longitudinally vittate. 23 species.

Sect. 9a. *Concinna* (Part 4(1), p. 61). Mature stem internodes 2-lined to terete, eglandular. Leaves free, entire, exappendiculate, usually conduplicate; laminar glands small, dense. Bracteoles entire, reduced. Flowers stellate. Perianth 5-merous. Sepal laminar glands linear. Anther gland amber. Capsule valves longitudinally vittate. One species.

Sect. 9b. *Graveolentia* (Part 4(3)). Mature stem internodes 2–4-lined and sometimes ancipitous above, nearly always terete below; eglandular or with dark (black) glands on or near lines or site of lines when young or scattered. Leaves free, entire, exappendiculate, plane or recurved; laminar glands dense to sparse. Bracteoles entire or with prominent marginal glands or basally glandular-ciliate. Flowers stellate. Perianth 5-merous. Sepal laminar glands linear to punctiform. Anther gland black or rarely amber. Capsule valves longitudinally vittate or rarely elongate- to ovoid-vesiculate, vesicles amber or rarely black. 9 species.

Sect. 9c. *Sampsonia* (Part 4(1), p. 63). Mature stems terete, eglandular. Leaves perfoliate, entire, exappendiculate, plane; laminar glands dense. Bracteoles entire, foliar or reduced. Flowers basally cupuliform. Perianth 5-merous. Sepal laminar glands striiform to punctiform. Anther gland black. Capsule valves elongate- to punctiform-vesiculate, vesicles amber. 2 species.

Sect. 9d. *Elodeoida* (Part 4(1), p. 66). Mature stem internodes terete or, when slender, 2-lined, eglandular. Leaves free, sometimes with gland-fringed auricles, occasionally lamina gland-fringed, plane; laminar glands relatively large, dense. Bracteoles often with gland-fringed auricles, reduced. Flowers stellate or rarely infundibuliform. Perianth 5-merous. Sepal laminar glands linear to punctiform. Anther gland black. Capsule valves longitudinally vittate. 5 species.

Sect. 9e. *Monanthema* (Part 4(1), p. 75). Mature stem internodes terete or, when slender, 2–4(6)-lined, eglandular or very rarely with reddish glands on lines. Leaves free, entire or gland-fringed and then with glandular-ciliate auricles, plane; laminar glands relatively small, sparse to occasionally dense. Bracteoles with gland-fringed auricles and reduced or entire and then usually foliar. Flowers stellate. Perianth 5(4)-merous. Sepal laminar glands linear to punctiform. Anther gland black. Capsule valves longitudinally vittate. 7 species.

The new taxa in the above summary are validated by the following diagnoses:

Sect. 9. ***Hypericum*** subsect. ***Hypericum*** series ***Senanensia*** N. Robson, **series nov.**: a series *Hypericum* caulibus demum teretibus lineis debilibus eglandularibus, differt.
Typus: *H. senanense* Maxim.

Sect. 9. ***Hypericum*** subsect. ***Erecta*** N. Robson, **subsect. nov.**: a subsect. *Hypericum* caudice lignoso stolonifero, internodiis caulium maturorum teretibus eglandularibus vel rarissime disperse rubiginoso-glandularibus, valvis capsularis semper longitudinaliter vittatis, differt.

Typus: *H. erectum* Thunb.

Sect. 9b. ***Graveolentia*** N. Robson, **sect. nov.**: a sect. *Hypericum* internodiis caulium maturorum persaepe basin versus teretibus, interdum eglandularis vel glandulis haud ad lineas prominentes limitatis, sepalorum glandulis laminaribus linearibus vel striiformibus vel raro punctiformibus, antherae glandula raro succinea, capsulae valvis longitudinaliter vittatis vel raro elongati- vel ovoidei-vesiculatis vesiculis rariore nigris, differt.
Typus: *H. graveolens* Buckley

Sect. 9c. ***Sampsonia*** N. Robson, **sect. nov.**: a sect. *Hypericum* internodiis caulium maturorum teretibus eglandularibus, foliis perfoliatis semper planis, floribus basi cupuliformibus, capsulae valvis disperse plusminusve elongati- vel punctiformi-vesiculatis, differt.
Typus: *H. sampsonii* Hance

Sect. 9d. ***Elodeoida*** N. Robson, **sect. nov.**: a sect. *Hypericum* internodiis caulium maturorum teretibus vel ubi tenuibus 2-lineatis eglandularibus, foliis interdum glanduloso-fimbriatis vel auriculatis auriculis glanduloso-fimbriatis, bracteolis semper glanduloso-fimbriatis, differt.
Typus: *H. elodeoides* Choisy

Sect. 9e. ***Monanthema*** N. Robson, **sect. nov.**: a sect. *Hypericum* internodiis caulium maturorum teretibus vel ubi tenuibus 2–4(6)-lineatis eglandularibus vel rarissime lineis rubroglanduliferibus, foliis interdum glanduloso-fimbriatis, bracteolis interdum glanduloso-fimbriatis, differt.
Typus: *H. monanthemum* Hook. f. & Thoms. ex Dyer

Key to sections, subsections and series in Part 4

1 Stamen fascicles and styles 5(4); black glands absent; shrubs, suffrutices or herbs 2

Stamen fascicles '3'('4'); styles 3(4); black glands nearly always present; suffrutices or herbs 3

2(1) Petals and stamens deciduous (sometimes tardily); shrubs or suffrutices ..... 3. **Ascyreia**

Petals and stamens persistent; herbs ..... 7. **Roscyna**

3(1) Leaf pairs perfoliate 4

Leaf pairs free 5

4(3) Flowers 27–40 mm in diam., stellate; styles appressed at base; capsule valves longitudinally vittate; black glands usually absent ..... 8. **Bupleuroides**

Flowers 6–15 mm in diam., substellate with cupuliform base; styles outcurving from base; capsule valves vesiculate; black glands present ..... 9c. **Sampsonia**

5(3) Leaves often conduplicate, very narrow (l:b = 4–10); anther gland amber; sepals imbricate ..... 9a. **Concinna**

Leaves plane or recurved, broad to narrow but l:b = < 4; anther gland black (rarely except in Sect. 9b) 6

6(5) Stem internodes persistently 2–4(6)-lined or -winged; dark glands on and usually confined to raised lines 7

Stem internodes terete or usually becoming terete; dark glands absent or not on raised lines 9

[2]Descending numbers of character values in descriptions show the presumed direction of evolution. Thus 5(4) indicates that 5 is the primitive number and is usual, but that a reduction to 4 sometimes occurs. On the other hand, 3(4) indicates merely that 3 is the usual number but that 4 sometimes occurs.

7(6) Bracts and bracteoles exauriculate; stems usually ± stout 8

Bracts and bracteoles auriculate; stems slender ..... 9e. **Monanthema** (part)

8(7) Sepal laminar glands striiform to punctiform; styles 2–6 mm long ..... 9. **Hypericum** subsect. 1. **Hypericum** series 1. **Hypericum**

Sepal laminar glands all or mostly linear; styles 5.6–12 mm long ..... 9b. **Graveolentia** (part)

9(6) Stem internodes with dark glands scattered or in 2 ranks 10

Stem internodes eglandular 11

10(9) Sepals obtuse to rounded; stems caespitose ..... 9. **Hypericum** subsect. 2. **Erecta** (part)

Sepals acute to obtuse or rarely rounded; stems creeping ..... 9b. **Graveolentia** (part)

11(9) Bracts and sometimes leaves with glandular or gland-fringed auricles 12

Bracts and leaves not auriculate; leaves and often bracts entire 13

12(11) Leaves with laminar glands relatively large, dense; lamina narrowly oblong to linear or if relatively broader, then to 10 mm pseudopetiolate ..... 9d. **Elodeoida**

Leaves with laminar glands relatively small, usually ± sparse; lamina broadly oblong to triangular-ovate or suborbicular or oblanceolate, up to 3 mm pseudopetiolate ..... 9e. **Monanthema** (part)

13(11) Bracts foliar; perianth 4-merous ..... 9e. **Monanthema** (part)

Bracts reduced; perianth 5-merous or variable (4–9-merous) 14

14(13) Rootstock herbaceous, stoloniferous; stems dispersed ..... 9. **Hypericum** subsect. 1. **Hypericum** series 2. **Senanensia**

Rootstock woody to fibrous, not stoloniferous; stems ± caespitose ..... 9. **Hypericum** subsect. 2. **Erecta** (part)

Sect. 7. Roscyna

Characters and variation (Figs 2, 3)

MORPHOLOGY. The species in sect. 3. *Ascyreia* to which *Hypericum ascyron* is most closely related appears to be *H. podocarpoides*, which is almost endemic to Nepal but also occurs in Kumaun (Uttar Pradesh). *H. ascyron* subsp. *ascyron* differs from it in its herbaceous habit with one or a few erect stems; its usually broader leaves with densely reticulate, tertiary venation, the pale glands striiform to punctiform in the areoles; its persistent petals and stamen fascicles; its larger flowers with relatively broad, usually obtuse sepals and spathulate to subunguiculate, often curved petals deflexed after flowering; its ± united styles; and its larger ovoid capsules. Although most of these characters are advanced relative to those of *H. podocarpoides*, the smaller flowers and condensed inflorescence axis of the latter species suggest that the relationship is not direct (Robson, 1985: 170, fig. 4).

Of the two derivative subspecies, subsp. *gebleri* is a plant of more northern or montane regions of eastern Asia with narrower, cuneate-based leaves, smaller flowers with narrower sepals and shorter free styles, and a narrower capsule broadest at the middle. Subsp. *pyramidatum*, on the other hand, is confined to north-eastern North America and differs from subsp. *ascyron* in its acute to acuminate sepals and almost free styles.

All three subspecies have 4-lined stem internodes and acute to obtuse leaf apex, whereas in the west Chinese *H. przewalskii* the internodes are partially 2-lined or wholly terete when mature, and the apex of the usually broader leaves is rounded to shallowly retuse.

Other variation in those taxa is discussed in the systematic treatment (pp. 52–61).

CYTOLOGY. Neither *H. podocarpoides* nor its near relative in sect. *Ascyreia*, *H. cordifolium* Choisy, has a known chromosome number. However, as the known diploid numbers in that section vary from 24 to 20, and 22 is very rare, the number of *H. podocarpoides* is likely

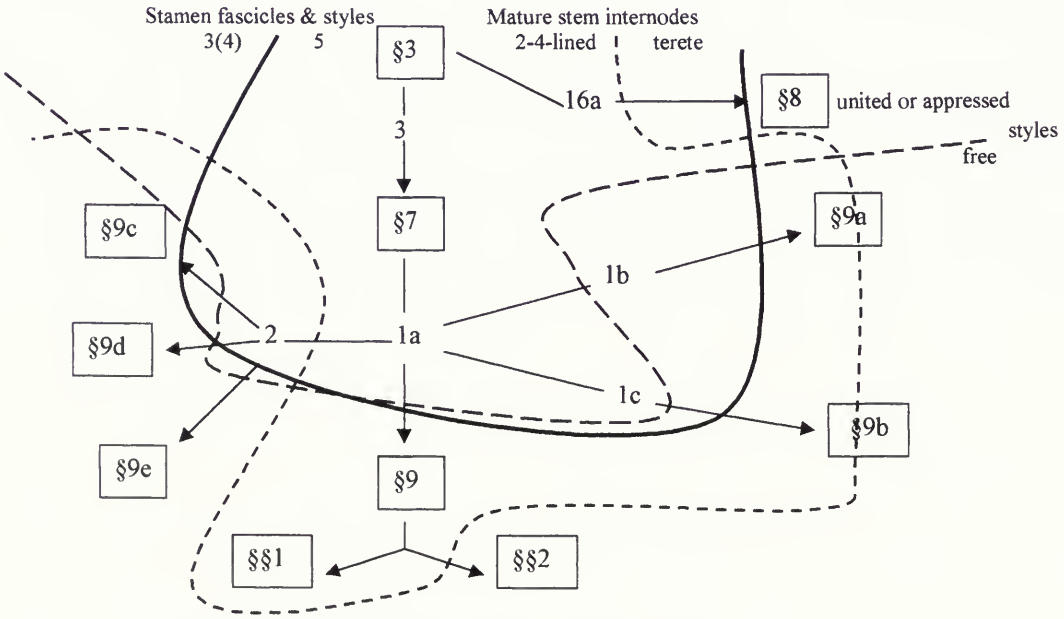


Fig. 3 Sections 7–9e. Limits of certain characters. For names of sections and species see Fig. 2 (p.•••).

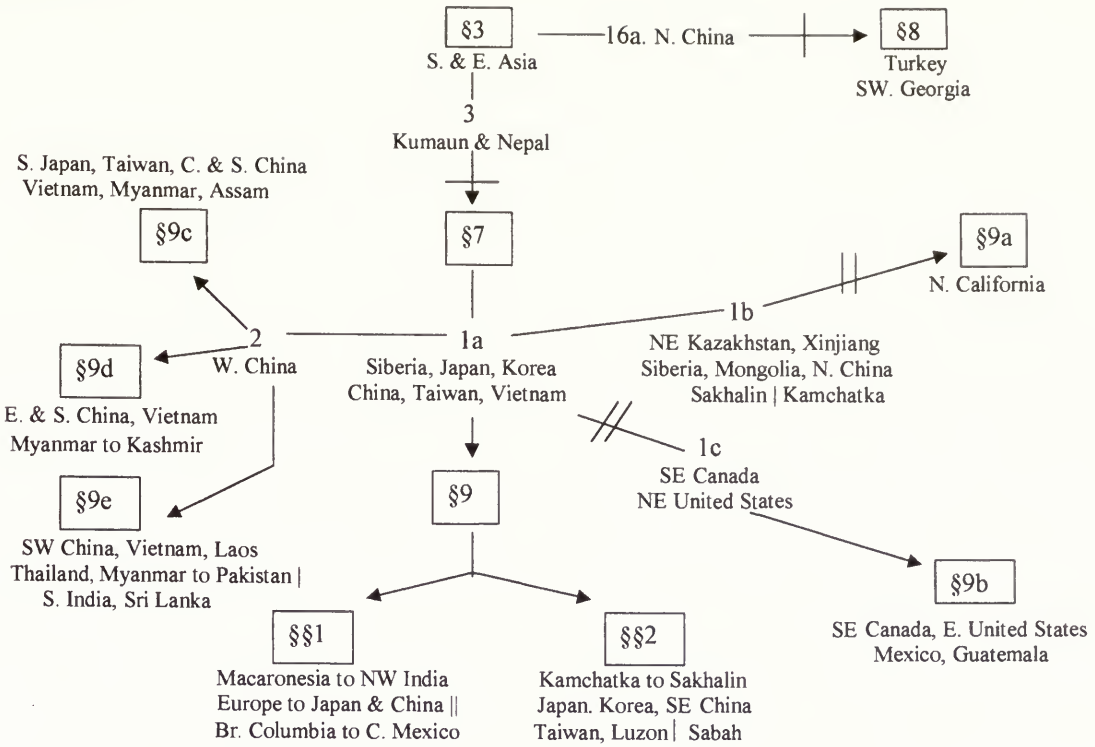


Fig. 4 Sections 7–9e. Distribution of species, showing major (||) and minor (|) disjunctions. For names of sections and species see Fig. 2 (p. 41).

to be 2n = 24 or 20 (see Fig. 2). For a long time *H. ascyron* subsp. *ascyron* was recorded as having only 2n = 18, but Russian workers have more recently shown it to have a range of numbers (16–22?), although 18 remains the usual one (*c.* 20–22, Krasnoborov et al., 1980; 16, Krogulevich, 1978). The only record for subsp. *gebleri* is also 2n = 18 (Stepanov, 1994). Chromosome numbers for subsp. *pyramidatum* and for *H. przewalskii* have yet to be determined. No hybrids of species in sect. *Roscyna* have been reported.

Distribution and evolution (Fig. 4)

The ranges of *H. podocarpoides* (Nepal) and its closest herbaceous relative *H. ascyron* subsp. *ascyron* (southern Siberia) are separated by the higher Himalayan range and the Tibetan Plateau, which were elevated as the result of the collision of the Indian subcontinent with the mainland in the late Paleocene or early Eocene, 55–60 m.y. B.P., and the gradual widening of the contact area eastward during the Eocene (Axelrod et al., 1998: 44). The subsequent elevation of the Tibetan Plateau resulted in the spread of grassland vegetation into this region (Hsü, 1983), an event that appears to have coincided with (caused?) the change in habit from shrub (*H. podocarpoides*) to herb (*H. ascyron*) and would have provided a suitable habitat for the latter. As the climate became increasingly desertified from the middle Miocene (15 m.y. B.P.) (Guo, 1981), the Tibetan Plateau would have become a barrier between the ranges of these species or their respective ancestors, confining *H. ascyron* to its northern rim in Siberia.

The subsequent spread of *H. ascyron* westward to the Altai Region and eastward as far as Kamchatka, and the development of a higher altitude/latitude subspecies (subsp. *gebleri*) requires no special hypothesis, even though the distribution of the latter is now to some extent disjunct. The occurrence of *H. ascyron* in north-eastern North America, however, could be explained by a migration either eastward across the Bering Bridge or westward across Europe and the Atlantic. No fossil evidence for its occurrence in Europe has been found and the breaking of the Atlantic Bridge in the late Cretaceous (*c.* 81 m.y. B.P.; Raven & Axelrod, 1974: 544) was too early to allow the passage of *H. ascyron* to America from the east, as was the latest possible time for direct overland migration across the North Atlantic (49 m.y. B.P.; McKenna, 1972). The Bering Bridge hypothesis is therefore to be preferred. The apparent evolution of subsp. *gebleri* from subsp. *ascyron* (and not *vice versa*), the postulated migration across the Bering Bridge of subsp. *gebleri* or the ancestor of *H. concinnum* is likely to have been later than the migration of subsp. *ascyron*. If so, this time difference would support the inference of Hui-lin Li (1952, cited by Kruckenberg, 1983: 594) that the western North American–eastern Asian disjunct group of species (in all families) is (i) more recent than the eastern North America–eastern Asian one and (ii) predominantly herbaceous rather than woody.

Sect. 9a. *Concinna*

The apparent relationship of *H. concinnum* to *H. ascyron* subsp. *gebleri* has already been shown in Fig. 2 and the distributional and evolutionary connections discussed on p. 41. These are shown in Figs 2–4. Note that the transition of the inner floral whorls from pentamery to pseudotrimery and trimery respectively again coincides (almost entirely) with a change of diploid number from 18 to 16 (Figs 2, 3).

Sects 9c. *Sampsonia*, 9d. *Elodeoida* and 9e. *Monanthema*

Characters and variation (Figs 5, 6)

MORPHOLOGY. Sects *Sampsonia*, *Elodeoida* and *Monanthema* (excepting the slender-stemmed species mentioned, p. 43) agree in having terete eglandular stem internodes but otherwise look very

distinct. Quite apart from the perfoliate leaves, subcupuliform corolla and vesiculate capsule of *Sampsonia*, its species have leaves and sepals that are entire with intramarginal black glands, the sepals being oblong-spathulate to linear and rounded and never foliose. The marginal glands of the petals are sometimes on cilia, whereas in *Elodeoida* they are never more than subsessile and in *Monanthemum* at most one glandular cilium occurs. In its mostly rather narrow leaves *H. sampsonii* resembles the more primitive, '*pedunculatum*' form of *H. przewalskii* (sect. *Roscyna*); but the 1–7 large flowers of that species are replaced by 20–40 small ones, the leaf pairs are united, not free, the stamen fascicles are pseudotrimerous and the ovary trimerous with free outcurving styles. The somewhat incurved petals are said by Momiyama (1982) to have 'raised fissures' (raised veins?) at the base, a feature that I have not been able to observe on dried material. The differences between *H. sampsonii* and *H. assamicum* (the other species in sect. *Sampsonia*) are mainly of size, but the ovary in the latter is said to be unilocular rather than trilocular, a character that, again, I have been unable to confirm.

The basic species of one clade of sect. *Elodeoida*, 1. *H. seniawinii*, also has the narrow leaves of the '*pedunculatum*' form of *H. przewalskii*, but the leaf pairs remain free and sessile, and their laminar glands are relatively large, round and dense, as in that form. The leaves in the other members of that clade (2. *H. petiolulatum* subsp. *yunnanense* (Franchet) N. Robson and subsp. *petiolulatum* respectively) become gradually smaller, relatively broad and, after developing a pseudopetiole, eventually suborbicular. The leaves, bracts and (usually) sepals remain entire. In the other clade, 3. *H. hengshanense* W.T. Wang also has narrow leaves with large, dense laminar glands; but the upper ones sometimes have marginal glandular cilia, which are constantly present in the bracts and sepals. Gland-fringed auricles, which are sometimes found in an early stage of development in *H. seniawinii*, are here constantly present in the upper leaves and bracts. The closely related 4. *H. elodeoides* is a usually smaller and acute-leaved derivative of *H. hengshanense* that has spread along the Himalayan range as far as Kashmir but is absent from Assam and Myanmar. The distributional gap is partly filled by subsp. *wardii* N. Robson, with obtuse to rounded leaves and a reversion to entire sepals and bracts. In the north of the same 'gap', in north Myanmar, Tibet and adjacent Arunachal Pradesh, is found a high alpine relative of subsp. *wardii* with much-branched stems, small broad leaves and irregularly gland-fringed to subentire sepals, *H. kingdonii* N. Robson.

Whereas sects *Sampsonia* and *Elodeoida* are related to the more primitive '*pedunculatum*' form of *H. przewalskii*, sect. *Monanthema* is clearly related to a broad-leaved form of that species in which the flowering branches are few or absent. In the south-western part of its range (in south-western Sichuan and adjacent Yunnan), *H. przewalskii* occurs as an extreme development of such a form, having an unbranched stem and only 1–3 flowers, in which the sepals tend to be foliose ('*H. macrosepalum*' Rehder). In addition, the laminar leaf glands tend to be smaller and less dense than in the '*pedunculatum*' form. All these characters, except foliose sepals, are found in the primitive (Yunnan) form of 1. *H. monanthemum* (1a. subsp. *monanthemum*); foliose sepals and bracts occur in 1b. *H. monanthemum* subsp. *filicaule* (Dyer) N. Robson. Small, more or less sparse laminar leaf glands are characteristic of the whole section.

Evolution in sect. *Monanthema* has apparently proceeded along three clades (Fig. 5). In the *Monanthemum* group the simple stem is retained until the later stages of development, e.g. the extreme small

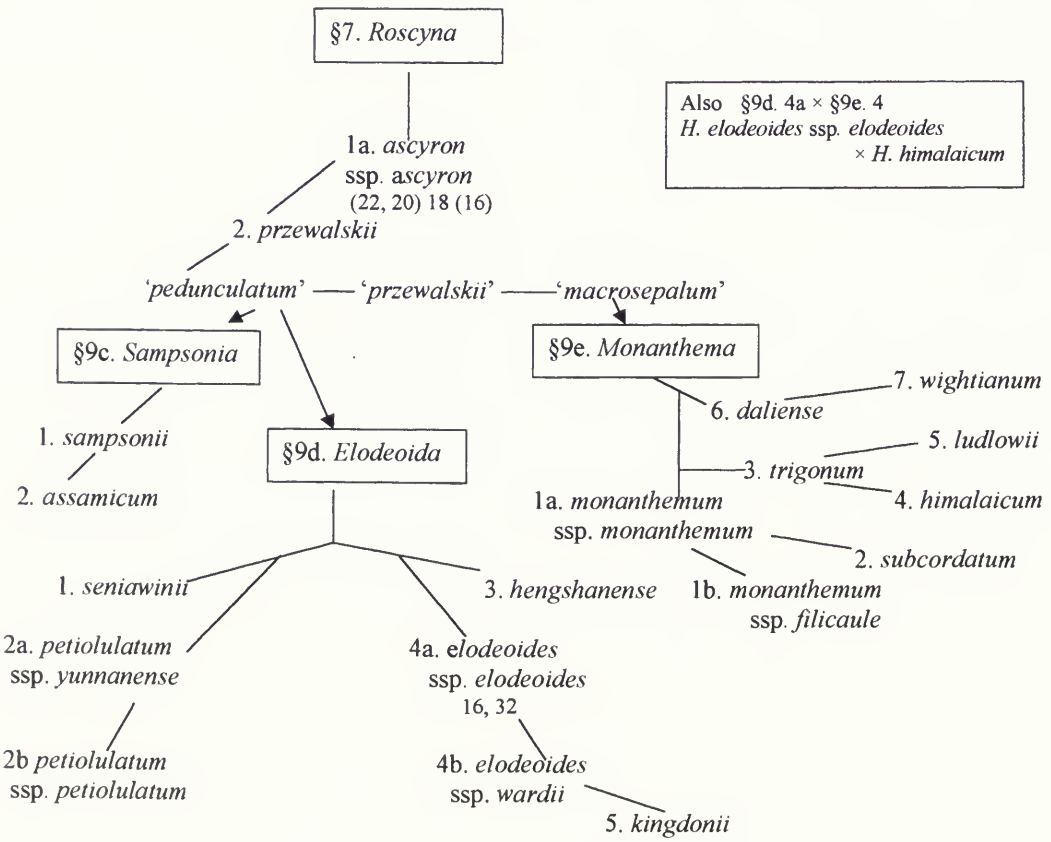


Fig. 5 Sections 9c–9e. Relationships, chromosome numbers (2n) and presumed hybrid.

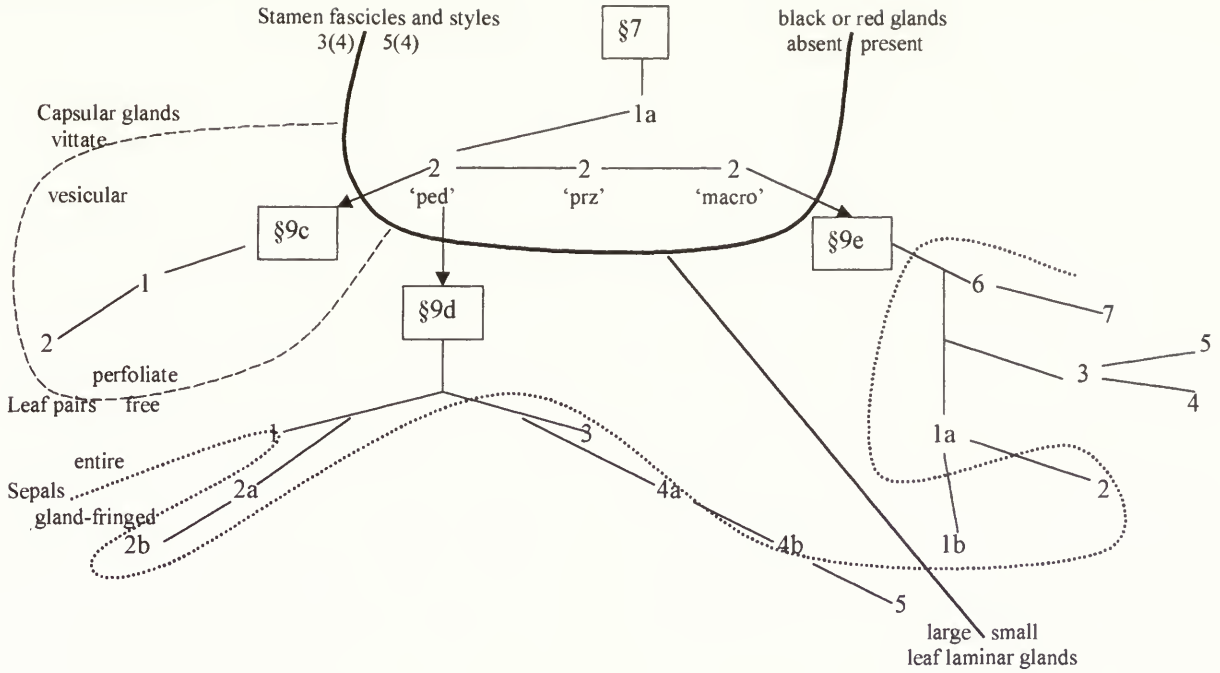


Fig. 6 Sections 9c–9e. Limits of certain characters. For names of sections and species see Fig. 5 (p. 46).

diffuse forms of 1b. *H. monanthemum* subsp. *filicaule*; here also the inflorescence is rarely more than 5-flowered and almost always from the terminal node only. The leaves and bracts are always entire, and the transition to 4-merous sepals and petals in *H. monanthemum* subsp. *filicaule* is accompanied by a return to entire (foliose) bracts and sepals. Extreme forms of this subspecies have a 2-merous ovary. In the other (northward) development of this clade, the slender-stemmed 2. *H. subcordatum* has also developed entire sepals, but these are not foliose.

In the other two clades of sect. *Monanthema* the inflorescence has become more branched, the branches more floriferous and the bracts and sometimes upper leaves auriculate. 3. *H. trigonum* Hand.-Mazz. (*Trigonum* group) is linked to *H. monanthemum* by a rather tall Sichuan population of the latter with an unbranched inflorescence but unusually long, slender styles. Its specific epithet refers to the triangular-ovate leaves that are characteristic of most of the group, as are glandular-ciliate bracts and sepals. There is, however, a reversion to entire sepals and bracts in extreme forms of 4. *H. himalaicum* N. Robson and the leaves in the *Trigonum* group are always entire. South of the Himalayan range, 4. *H. himalaicum* has developed from *H. trigonum* with smaller leaves and flowers and shorter styles, relatively and absolutely. To the north of that range, *H. trigonum* has given rise to 5. *H. ludlowii* N. Robson, in which the more erect stem has shorter branches and the small flowers have relatively longer styles, achieved by a greater reduction in the size of the ovary than in the length of the styles themselves. The frequency of red 'dark glands' in this species indicates a diminution in the concentration of hypericin, as was seen in *H. elodes* L. (sect. 28. *Elodes*; Part 6, *Robson*, 1996: 209).

The third clade of sect. *Monanthemum* consists of two species, the widespread 7. *H. wightianum* Wall. ex Wight & Arn. and an endemic of the Dali and Lijiang ranges in Yunnan, 6. *H. daliense* N. Robson. In both these species the few- and large-flowered inflorescence of *H. przewalskii* and *H. monanthemum* is replaced by one with numerous small flowers; but the elliptic-oblong leaves are the most similar in this section to those of *H. przewalskii* ('*macrosepalum*' form). This clade is unlikely, therefore, to have been derived from either of the others (Fig. 5). Other developments in this clade that are unique in the section include the frequent occurrence of (a) a complete or basal glandular-ciliate margin in the upper leaves of *H. wightianum* and (b) marginal black glands between the glandular cilia in the sepals of both species but particularly those of *H. wightianum*. As in the *Trigonum* group, the bracts are glandular-auriculate and in the present group so are the gland-fringed leaves. The glandular fringes of the sepals vary from denticulate (in *H. daliense*) to ciliate and laciniate (in most of *H. wightianum*); but in the extremely reduced form of the latter species in south India and Sri Lanka, there is a reversion to entire sepals and bracts. The additional development of shortly petiolate leaves in this form has given rise to a plant that has been confused with the European *H. humifusum* L. (sect. 15. *Oligostema*) ever since the account of *Hypericum* was published in the *Flora of British India* (Dyer, 1874).

CYTOLOGY. Practically no cytological data have been published on species in sects 9c–e. Chromosome counts have been made only on *H. elodeoides* (sect. 9d. *Elodeoida*), which has diploid and tetraploid populations on the base 8, i.e. 2n = 16, 32. No evidence regarding an association of this difference of ploidy level with morphological characters is available.

Distribution and evolution (Fig. 7)

9C. SAMPSONIA. With its distinctive perfoliate leaf pairs, elongate entire sepals and vesiculate capsules, sect. *Sampsonia* would appear to have been an early development from *H. przewalskii* '*pedunculatum*' (clade i); and the wide distribution of its main species, *H. sampsonii*, supports this idea. From a notional origin in west China (based on the present variation and distribution of *H. przewalskii*), it has spread north to eastern Gansu and Jiangsu, east to southern Japan and Taiwan, and south to the rest of China and extreme north Vietnam. Unlike members of sects 9d and 9e, it has not penetrated

into Yunnan or the Himalayan massif but is found in eastern Myanmar; the very closely related *H. assamicum* extends the sectional distribution to Meghalaya.

9D. ELODEOIDA. The other two sections are more similar to each other than either is to sect. 9c, even though the morphological evidence suggests that 9d is related to '*pedunculatum*', whereas the affinities of 9e are with '*macrosepalum*'. The basic species in one clade (clade ii) of sect. *Elodeoida*, 1. *H. seniawinii*, has a rather similar mainland distribution to that of *H. sampsonii*, but is absent from Japan and Taiwan. To the west it intergrades geographically, though not morphologically, with 2a. *H. petiolulatum* subsp. *yunnanense*, the area of overlap including parts of Henan, Hubei, Hunan, Jiangxi, Guangxi and Guizhou. Subsp. *yunnanense* in turn is replaced in Sichuan and Yunnan by 2b. *H. petiolulatum* subsp. *petiolulatum*, which is distributed through the main Himalayan range to Nepal.

The other clade (clade iii) has two closely related taxa at the base. 3. *H. hengshanense* has a limited relict distribution in south-east China (Jiangxi, Guangdong and northern Guangxi), whereas the more variable and morphologically more advanced 4a. *H. elodeoides* subsp. *elodeoides* occurs throughout southern China from Fujian, Jiangxi, Hubei and Sichuan southward and extends along the main Himalayan range as far as Kashmir and into Meghalaya. Although its range in China includes all that of *H. hengshanense*, this overlap should be interpreted as resulting from an invasion by *H. elodeoides* from the west, because the Chinese plants are morphologically advanced, the most primitive forms being in the central Himalaya. The other subspecies, 4b. *H. elodeoides* subsp. *wardii*, is a southward development into Manipur and central Myanmar (Mt. Victoria); this seems to have given rise to a small plant of extreme northern Myanmar, adjacent Xizang and extreme eastern Arunachal Pradesh, 5. *H. kingdonii*.

9E. MONANTHEMA. This section is related to the most advanced form of *H. przewalskii* from the southwestern-most part of its range (Sichuan and northern Yunnan), '*H. macrosepalum*'; the basic species of all three of its clades occur in or near this region. The basic taxon of clade iv, 1a. *H. monanthemum* subsp. *monanthemum*, has its most primitive form in northern Yunnan and has spread out to both south-west and north-east. South-westward there is a reduction trend in size through Yunnan and along the Himalayan range to Nepal, where there are some plants intermediate in form between it and 1b. *H. monanthemum* subsp. *filicaule*. This latter subspecies then shows a reduction trend in the opposite direction through Xizang and ending in Yunnan. North-eastward from northern Yunnan and through south-eastern Sichuan subsp. *monanthemum* remains almost uniform, but there is a distinct morphological gap between it and the delicate derivative 2. *H. subcordatum*, which extends south in area from its centre in southern Shaanxi as far as Emei Shan.

The second clade, clade v, originates in a species from a small area in north-west Yunnan, 3. *H. trigonum*, which is morphologically very similar to the form of 1. *H. monanthemum* from nearby. It has given rise to two species. To the south of the main Himalayan range, 4. *H. himalaicum* occurs in the Arunachal Pradesh–Myanmar frontier area, then recurs in central Nepal, whence it shows trends both westward to Pakistan and eastward to Sikkim, then through the Chumbi gap into Xizang and thence into Yunnan. To the north of the main range, 5. *H. ludlowii* shows a reduction trend in size from north-western Yunnan through Xizang into Bhutan.

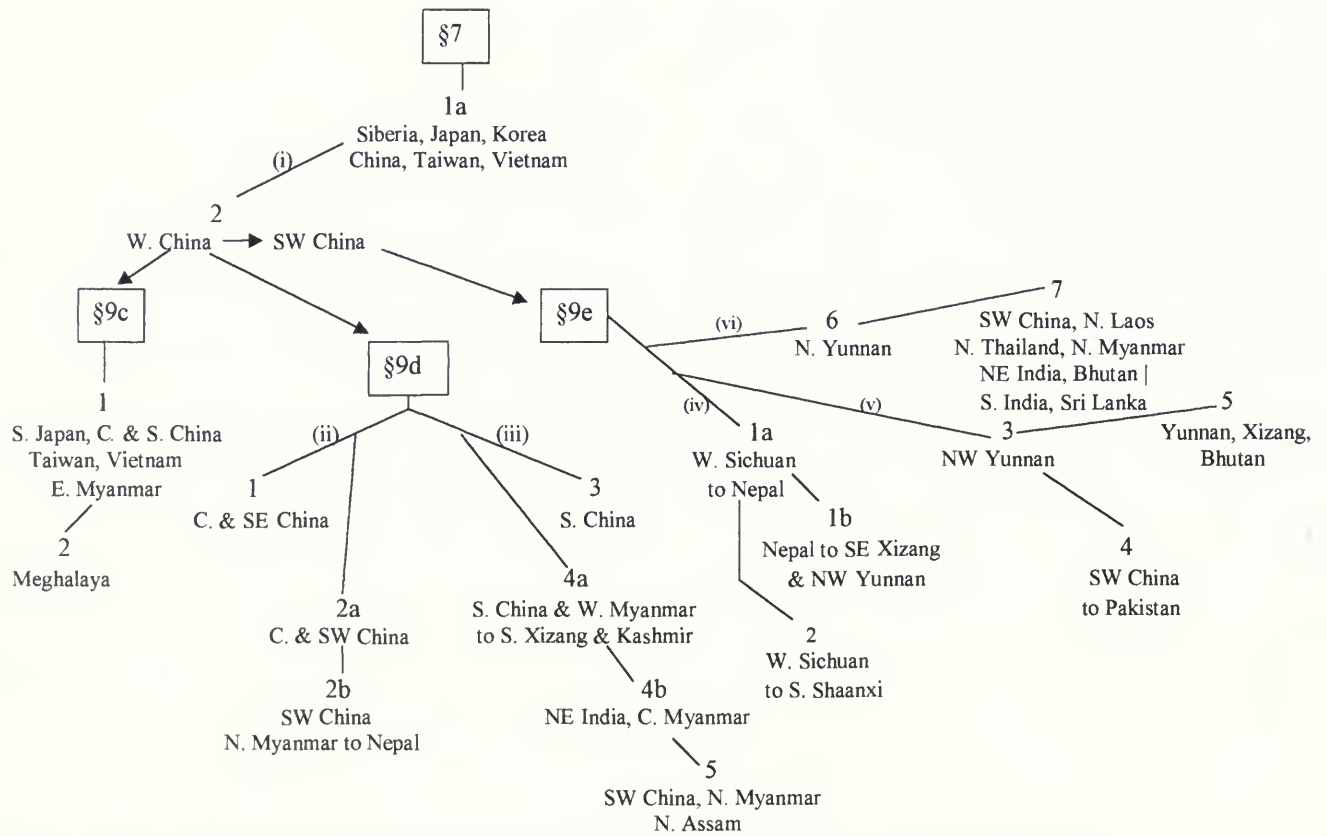


Fig. 7 Sections 9c–9e. Distribution of species, showing minor disjunction (|). For names of sections and species see Fig. 5 (p. 46).

Finally, clade vi originates in 6. *H. daliense*, a relict endemic of the Dali and Lijiang ranges of northern Yunnan. It is closely related (ancestral?) to the widespread 7. *H. wightianum*, of which the most similar form to *H. daliense* occurs in the Khasi Hills (Meghalaya). From there reduction trends are found: (a) westward to Sikkim; (b) eastward into China as far as Guanxi, Guizhou and Sichuan; (c) southward into Nagaland and Mizoram (eastern India) and, with a large disjunction, in Tamil Nadu and Sri Lanka; (d) from northern Myanmar into central Myanmar and northern Thailand.

SYSTEMATIC TREATMENT[3]

Sect. 3. **ASCYREIA** Choisy – an additional species (see p. 40).

16a. **Hypericum elatoides** R. Keller in *Bot. Jb.* **33**: 549 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 588 ['*helatoides*'], 590 (1908); N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 320 (1977) sub sect. *Roscyna*; Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 71 (1990). Type: China, Shensi [Shaanxi] settentr., Ki-san, May 1895 (fl), *Scallan* in *Biondi* 3822 (FI!–holotype).

Fig. 8A, Map 1.

H. monogynum var. *franchetii* Baroni [*Enum. Sem. in Horto bot. Florent. anno 1898 coll.*: 36 (1898?)] in *Boll. Soc. Bot. Ital.* 1898: 185 (1898), *Diagn. Pl. Sin. Nov.*: 35 (1898). Type: Cultivated in Hort. bot. Florentino ex China, Shaanxi, 1894 ex Giraldi, July 1895 (fl), *Herb. Biondi* 3809 (FI!–lectotype, selected here).

H. chinense sensu R. Keller in *Bot. Jb.* **33**: 548 (1904) pro parte quoad specim. cit.

H. ascyron var. *punctato-striatum* R. Keller in *Bot. Jb.* **33**: 550 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 592 (1908). Type: China, Shen-si [Shaanxi], presso la cima di In-kia-po, 4 June 1897 (fl), *Giraldi* in *Biondi* 3816 (FI!–lectotype, selected here).

H. ascyron var. *micropetalum* sensu R. Keller in *Bot. Jb.* **33**: 550 (1904) pro parte quoad specim. cit.; H. Léveillé in *Bull. Soc. Bot. France* **54**: 592 (1908).

Suffrutex 0.35–0.82 m tall, with stems solitary or few, usually slender, erect from ascending or creeping, branching and rooting base, unbranched below inflorescence. *Stems* shallowly 4-lined below nodes, sometimes 2-lined below or becoming almost terete, eglandular; internodes (30–)45–105 mm, shorter than or equalling leaves. *Leaves* sessile or with petiole to 1.5 mm; lamina 44–110 × 18–50 mm, oblong or oblong-triangular to broadly ovate, rather paler beneath, not glaucous, plane, thinly chartaceous; apex obtuse to shortly apiculate or rounded, margin entire, base cordate-amplexicaul to truncate; venation: 4–7 pairs of main lateral veins from lower half of midrib, tertiary reticulation dense, prominent below; laminar glands very small, striiform to punctiform; intramarginal glands dense. *Inflorescence* (1–)5–13-flowered, from 1–2 nodes, rarely with flowering branches from one node below, the whole laxly corymbiform; pedicels (3–)10–50 mm; bracts and bracteoles 7–17 mm long, linear-lanceolate to linear-elliptic. *Flowers* 40–80 mm in diam., stellate, with petals becoming reflexed, tardily deciduous; buds narrowly ovoid, ± acute. *Sepals* 5, free or to 0.25 united, slightly imbricate, 3–5(–7) × 1.5–3(–5) mm, ovate to triangular-ovate, obtuse to acute, entire or occasionally minutely irregularly glandular-ciliate, erect to suberect in bud and fruit; veins 5, branched; laminar glands linear (inner) or interrupted (outer); marginal glands reddish or absent. *Petals* 5, golden? yellow, 25–40 × 7–10(–15) mm, 6–8 × sepals, oblanceolate, without apiculus, margin entire; laminar glands linear to distally striiform. *Stamen fascicles* 5, each with *c.* 45–60 stamens, longest 15–25 mm long, 0.5–0.65 × petals; anthers yellow, gland amber. *Ovary* incompletely 5-locular, 4–6(–7) × 3.5–4.5 mm, ± broadly ovoid; styles 5, 13–17 mm, 2.3–4.5 × ovary, slender, united almost to apices; stigmas small. *Capsule* 9–16 × 6–11 mm, broadly to narrowly ovoid or ovoid-conic, 3–4 × sepals, evittate. *Seeds* dark reddish brown, 1.1–1.5 mm, cylindric, without terminal appendage, very shallowly carinate; testa densely shallowly reticulate. 2n = ?

Damp places in open grassland; 770–1000 m.

China (Henan, Shaanxi, Gansu).

CHINA. Henan: Neixiang Xian, Baotianman Nat. Res., Xuayao Gou, 850–950 m, 22 May 1994 (fl), *Boufford* et al. 26156 (BM, GH*). **Shaanxi**: Danfeng Xian, Yaozhuang, Dadongqiu, 1000 m, 20 September 1958 (fr), *Guo B.Z.* 3873 (BM – photo, IBSC, KUN)); Tai-pei-shan [Taibaishan], 1910 (fl), *Purdom* 893 (A*, E, K, US); Tsincheng-hsien [Xinchengbu? Xian], Taihangshan, 820 m, 19 June 1937 (e. fr), *Liou* 7343 (BM – photo, PE); Lao-y-san presso Zu-lu, 6 September 1897 (fr), *Giraldi* in *Biondi* 3818 (FI; K). **Gansu**: Tangye to Wushang Xian, 3 June 1956 (fl), *Huang He Exped.* 4465 (BM – photo, PE).

H. elatoides is most closely related to *H. monogynum*, in particular to an ovate- to oblong-leaved form from Jiangsu (e.g. *Wilson* 1604). It differs from Form III of *H. monogynum* (e.g. *Wilson* 2420, from west Hubei), by the suffruticose habit, the larger thinner leaves, the usually 2-noded inflorescence, the relatively short and broad sepals with a thinner, usually glandular-ciliate margin, the tardily deciduous exapiculate petals and the more numerous, tardily deciduous stamens. It is rather similar to *H. prattii* N. Robson (from Sichuan), but differs from it by the obtuse to rounded (not acute to apiculate) relatively narrow leaves and the small triangular-ovate, usually minutely reddish-glandular-ciliate sepals. In *H. prattii* the sepals are large and ovate-lanceolate to elliptic with an entire margin.

Sect. 8. **BUPLEUROIDES** Stef. in *God. Agr.-les. Fak. Univ. Sofiya* **11**: 160 (1933).

Perennial herbs up to 0.75 m tall, with stems erect from branching rhizome, glabrous, without dark glands or, if present, then small, reddish or black, and marginal only. *Stems* incompletely 2-lined or usually terete, eglandular. *Leaves* opposite, perfoliate, persistent; lamina entire with venation pinnate, closed, the tertiary reticulation dense; laminar glands pale, small, punctiform, scattered; marginal gland dots irregular, small; ventral resin glands absent. *Inflorescence* 4–25-flowered with branching dichasial/monochasial from 1–5 nodes, without subsidiary branches; bracts and bracteoles persistent. *Flowers* stellate or with petals reflexed, homostylous. *Sepals* 5, free, persistent, erect in bud and fruit, with margin entire or minutely glandular; veins 5; laminar glands pale, linear or striiform to sometimes punctiform; marginal glands reddish to black or absent. *Petals* 5, persistent, without apiculus, entire or usually with minute sessile, reddish to black marginal glands; laminar glands pale, ± numerous, striiform to punctiform. *Stamen fascicles* 4 (united 2+1+1+1) or usually 3 (united 2+2+1), persistent, the single ones

[3]An asterisk (*) before a locality or after a herbarium symbol indicates that the specimen has not been seen by me. Type material seen by me is indicated by an exclamation mark (!).

each with *c.* 20–25? stamens; filaments united at base only; anthers yellow, gland amber; pollen type IV. *Ovary* with 3(4) placentae, wholly united, ∞-ovulate; styles 3(4), free, appressed below; stigmas small. *Capsule* 3(4)-valved, coriaceous, with valves narrowly longitudinally vittate. *Seeds* ± curved-cylindric, not or slightly carinate, without apical expansion; testa shallowly and minutely foveolate.

BASIC CHROMOSOME NUMBER (X). Unknown.

HABITAT. Damp places in forest; 1000–2100 m.

DISTRIBUTION. North-east Turkey, Georgia.

1. **Hypericum bupleuroides** Griseb. in Wiegm., *Arch. Naturgesch. (Berlin)* **18**(1): 299, in obs. (1852); Boiss., *Fl. orient.* **1**: 809 (1867); Woronow in Kuzn., Busch & Fomin, *Fl. Caucasica Critica* **3**, No. 9: 47 (1906); Stefanoff in *God. Agr.-les. Fak. Univ. Sofiya* **10**: t. 1 f. 11 (1932), **11**: 160 (1933), **12**: 84 (1934), in *Pflanzenareale* **4**: karte 2b (1933); Gorschkova in Shishkin & Bobrov, *Fl. URSS* **15**: 246 (1949); Grossgeim, *Fl. Kavk.* 2nd ed. **6**: 174, map 193 (1962); N. Robson in Davis, *Fl. Turkey* **2**: 367 (1967). Type as for *H. perfoliatum* Ledeb.

Fig. 8B, Map 2.

H. perfoliatum Ledeb. in *Bull. Acad. Sci. St. Petersb.* **2**: 314 (1837), *Fl. Ross.* **1**: 445 (1842), non L. (1767). Type: Georgia, auf dem Hochplateau Gor-Somlia zwischen der provinz Guriel und Adschara, 1500–2100 m, 1836 (fl), *von Nordmann* s.n. (LE-lectotype & syntype; H!). There are two Helsinki specimens: (i) Mont Adzhar, Guriel (isolectotype, selected here) and (ii) Akhalziki [Achaltsikhe] (isosyntype).

Perennial herb, 0.45–0.8 m tall, with stems solitary or few, erect from creeping and rooting base, unbranched below inflorescence. *Stems* incompletely 2-lined or usually terete, eglandular; internodes 50–120 mm, shorter to longer than leaves. *Leaves* perfoliate, with or without ± shallow sinus at points of union; lamina 70–210(280) × 37–80(–100) mm, ovate to elliptic-ovate or oblong-ovate, paler beneath, not glaucous, plane, papyraceous; apex obtuse to apiculate, margin entire, bases united in pairs; venation: 4 pairs of main lateral veins from lower third or so of midrib, tertiary reticulation dense, only main veins prominent beneath; laminar glands pale, very small, scattered; marginal glands pale, small, irregular. *Inflorescence* 4–11(–25)-flowered, from 1–3 nodes, without flowering branches, the whole ± broadly pyramidal; pedicels 18–25 mm; bracts and bracteoles 0.5–4 mm long, lanceolate, withering and falling, leaving scale-like base. *Flowers* 27–40 mm in diam., stellate, with petals becoming reflexed; buds narrowly ovoid?, rounded? *Sepals* free, narrowly imbricate, unequal, 2.5–4.5 × 2–2.3 mm, elliptic-oblong to ovate, rounded, entire or with minute sessile glands, erect in bud and fruit; veins 5, distally branched; laminar glands linear to striiform or distally punctiform; marginal glands reddish to black or absent. *Petals* 15–20 × 2.5–5? mm, *c.* 8 × sepals, narrowly oblanceolate, without apiculus, entire or usually with minute sessile glands; laminar glands pale, striiform to punctiform; marginal glands reddish to black. *Stamens* 50–75, longest 14–17 mm long, *c.* 0.75–0.85 × petals; anther gland amber. *Ovary* (3.5?–)6–7 × 3 mm, ovoid-conic; styles 12–14 mm, 2–3 × ovary, slender; stigmas small. *Capsule* 9–14 × 5–8 mm, ellipsoid to ovoid, *c.* 3.5 × sepals, narrowly longitudinally vittate. *Seeds* reddish brown, 1.2–1.5 mm, ± cylindric, slightly curved, without terminal appendage, not or slightly carinate; testa minutely linear-foveolate. 2n = ?

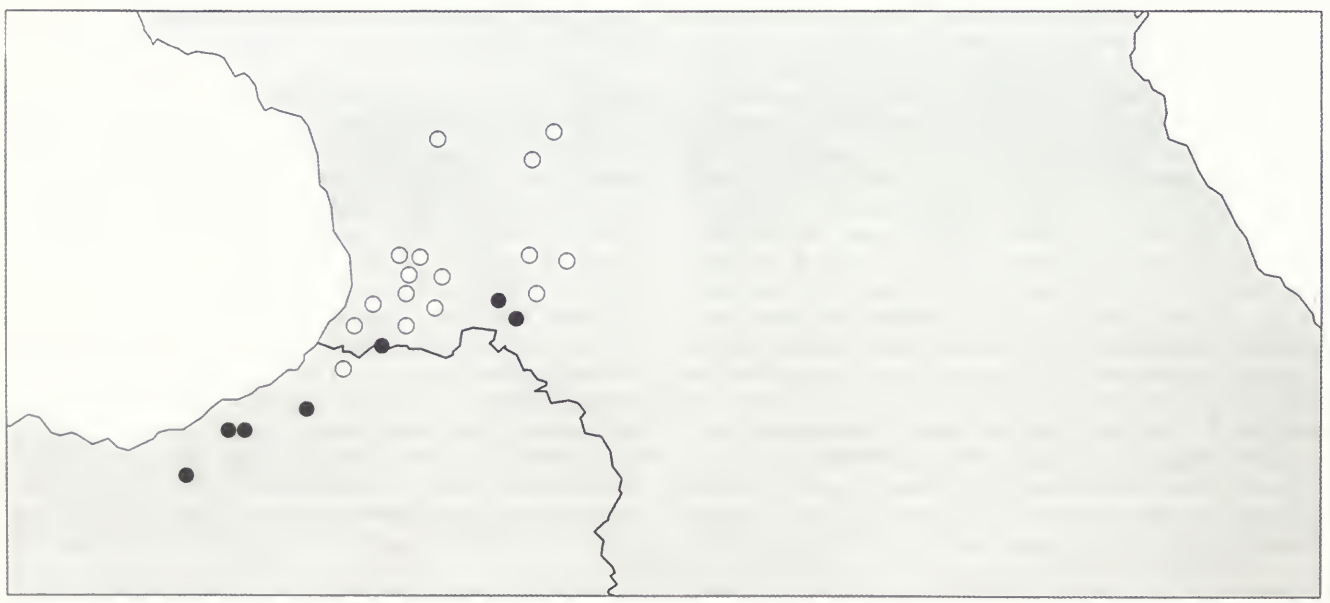
Mountain woods and damp valleys, wooded slopes; 640–2100 m.

North-east Turkey (Rize, Çoruh), Georgia.

TURKEY. **Rize**: Hemsin Distr., Meydan Kobaca to Mollaveysa, 1000 m, 3 September 1952 (l. fl), *Davis & Dodds* D21372 (BM, E, K); Ikizdere nach Çamlik, 1200 m, 13 July 1958 (fl), *Huber-Morath* 14974 (BASBG); gorges 10 km below Khabakhor (Lazistan), *c.* 1000 m, 27 August 1866 (fr), *Balansa* 89 (E, G, JE, K). **Çoruh**: inter Salaket et Khinzart, *c.* 1350 m, 6 August 1911 (fl), *Woronow* 5670 (JE, K, S); Šavval Tepe above Murgul, 1600 m (to 1900 m), 11 August 1957 (l. fl), *Davis & Hedge* D.32223 (BM, E, K).

GEORGIA. **Adzharskaya**: basin of R. Kableani, Kishlak village, August 1948 (fl), *Sochava & Naumova* s.n. (LE); Batumi, Mtirala Mtn, 640 m, 14 July 1975 (l. fl), *Whitmore* 3100 (BM). **Georgia**: Mt. Imeretia inter Kutais et Achalzich, n.d., *Ruprecht* s.n. (G).

H. bupleuroides is an isolated Tertiary relict (Woronov, 1906: 48) of which the nearest relative is in central China (*H. elatoides*, sect. *Ascyreia*; see p. 40) and provides a morphological link between it and *H. monogynum*. *H. xylosteifolium* (Spach) N. Robson (sect. 6.



Map 2 Sect. 8: 1. *H. bupleuroides* ● specimens, other records ○.

Fig. 8 A. H. *elatoides*: (a) habit; (b) sepal; (c) petal; (d) ovary; (e) capsule. B. *H. bupleuroides*: (f) habit; (g) sepal; (h) petal; (i) ovary; (j) capsule (a, f × 2/3; c-e, h-j × 2; b, g × 4). A. (a), (d) *Purdom* 893; (c) *Wang* 3694; (e) *Fr. Hugh* s. n. B. (f)–(i) *Whitmore* 3100; (j) *Davis & Hedge* 32223.

Inodora), which provides another example of this disjunction between central China and the south-east Black Sea region, is also a Tertiary relict with no close relatives, its nearest one being the variable *H. monogynum* (see Robson, 1985: 314).

H. bupleuroides differs from *H. elatoides* in its herbaceous habit, perfoliate leaves, pseudo-trimery in the androecium and trimery in the gynoecium. In addition, the styles are only loosely appressed in the lower half, not almost completely united.

Sect. 7. **ROSCYNA** (Spach) R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* **3**(6): 211 (1893); N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 319 (1977) pro parte, excl. *H. elatoides* R. Keller.

Perennial herbs up to 2 m tall, with stems erect or sometimes basally ascending from taproot, glabrous, without dark glands; branching lateral, confined to inflorescence or from up to all nodes. *Stems* 4–2-lined when young, becoming narrowly 4-winged to terete, eglandular. *Leaves* opposite, decussate, sessile to subsessile, free, persistent; lamina entire with venation pinnate, closed sometimes except lower 1–2 pairs, with tertiary reticulation dense, sometimes obscure; laminar glands pale, punctiform or shortly striiform, unequal; marginal gland dots dense, very small; ventral resin glands absent. *Inflorescence* 1–*c.* 35-flowered with branching dichasial/monochasial from 1–7 nodes, often with subsidiary branches from lower nodes; bracts and bracteoles foliar or reduced, deciduous or persistent. *Flowers* stellate, homostylous. *Sepals* 5, free or united at base, persistent, spreading to deflexed in fruit, with margin entire; veins 5–17; laminar glands linear and distally interrupted to striiform or wholly punctiform; intramarginal glands few or absent. *Petals* 5, persistent and becoming reflexed, with apiculus present, lateral, or absent; margin entire; marginal glands absent; laminar glands linear, sometimes interrupted distally, numerous, or rarely absent. *Stamen fascicles* 5, free (or 4?, united 2+1+1+1), persistent, each single fascicle with *c.* 15–30 stamens; filaments united at base only; anthers yellow, gland amber; pollen type III. *Ovary* with central lacuna and 5(4) axile placentae, ∞-ovulate; styles 5(4), partly united or partly coherent or free; stigma narrowly to broadly capitate or infundibuliform. *Capsule* 5(4)-valved, coriaceous, with valves narrowly longitudinally vittate. *Seeds* cylindric, narrowly carinate to narrowly winged, sometimes with slight apical expansion; testa densely and shallowly linear-reticulate.

BASIC CHROMOSOME NUMBER (X). 11–10? (see p. 44), 9, 8; ploidy 2.

HABITAT. Moist to dry meadows or grassy or rocky slopes, in open forest or among scrub or along streamsides and river banks, also along roadsides; 0–4000 m.

DISTRIBUTION. Siberia (Altai to Kamchatka and Kurile Is., Sakhalin), Mongolia, Korea, China (all provinces except Xizang and Qinghai), Vietnam (north), Taiwan, Japan; Canada (south-east), U.S.A. (north-east).

2 species (+ 2 subspecies).

Key to sect. 7. *Roscyna*

1 Leaf apex acute to obtuse, lamina mostly lanceolate to elliptic-oblong or linear; mature stem internodes sharply 4-lined to narrowly 4-winged (1. **ascyron**) 2

Leaf apex rounded to shallowly retuse, lamina oblong to oblong-lanceolate or oblong-ovate or triangular-oblong; mature stem internodes partially 2-lined or terete ..... 2. **przewalskii**

2(1) Capsule ovoid to ovoid-pyramidal or ovoid-cylindric; sepals 6–13 mm wide, ovate to lanceolate or oblong or elliptic; styles 4–15 mm, *c.* 0.7–2 × ovary, almost free to up to 0.8 united; leaves *c.* 7–40 mm wide, base cordate to rounded 3

Capsule cylindric-ellipsoid; sepals 1.5–7 mm wide, narrowly oblong or oblong-lanceolate; styles 2.5–3.5 mm, *c.* 0.5 × ovary, free; leaves 4–15 mm wide, base usually cuneate ..... 1b. **ascyron** subsp. **gebleri**

3(2) Sepals rounded to obtuse or rarely acute; styles usually ± united ..... 1a. **ascyron** subsp. **ascyron**

Sepals acute to shortly acuminate; styles usually almost free ..... 1c. **ascyron** subsp. **pyramidatum**

1. **Hypericum ascyron** L., *Sp. pl.*: 783 (1753) excl. syn. Moris. et Wheeler. et Ray. et loc. Oriente; Murray, *Syst. veg.* 13th ed.: 583 (1774); Lam., *Encycl.* **4**: 147 (1796); Willd., *Sp. pl.* **3**: 1443 (1802); Choisy, *Prodr. monogr. Hypéric.*: 41 (1821), in DC., *Prodr.* **1**: 545 (1824); Sprengel, *Syst. Veg.* **3**: 342 (1826); G. Don, *Gen. Syst.*: 602 (1831); Ledeb., *Fl. altaic.* **3**: 363 (1831), *Fl. ross.* **1**: 446 (1842); Turcz., *Fl. Baic.-Dah.* **1**: 621 (1843); Maxim., *Prim. fl. amur.*: 64 (1859); Regel, *Fl. ussur.*: 32 (1861); Trev., *Hyperic. animadv.*: 8 (1861); Miquel in *Ann. Mus. Bot. Lugduno-Batavum* **2**: 250 (1866); Franchet & Sav., *Enum. Pl. Jap.* **1**: 55 (1874); Tanaka in Înuma, *Sômoku-Zusetsu*, 2nd ed., **14**: t. 33 (1874); Hance in *J. Bot., Lond.* **18**: 259 (1880); Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 430 (1882), *Mél. Biol.* **11**: 163 (1882); Franchet in *Nouv. Arch. Mus. Hist. Nat.*, 2e sér., **5**: 207 (1883), *Pl. Dav.*: 55 (1884), in *Bull. Soc. Bot. France* **33**: 436 (1886); Hemsley in *J. Linn Soc.* **23**: 72 (1886); Franchet, *Pl. delavay.*: 112 (1889); Korschinsky in *Acta Hort. Petrop.* **12**: 317 (1892); Goeschke in *Gartenflora* **41**: 537, t. 1381 (1892); R. Keller in *Bull. Herb. Boiss.* **5**: 638 (1897); Diels in *Bot. Jb.* **29**: 476 (1900); Krylov., *Fl. Altaya* **1**: 188 (1901); Komarov, *Fl. Man'chzh.* **3**: 40 (1905); Matsum. & Hayata, *Enum. pl. formosa*: 40 (1906); H. Léveillé in *Bull. Soc. Bot. France* **53**: 498 (1906), op. cit. **54**: 592 (1908); Pavolini in *Nuovo Giorn. Bot. Ital.*, n. ser. **15**: 406 (1908); Nakai, *Fl. kor.* **1**: 95 (1909); R. Keller in *Bot. Jb.* **44**: 48 (1909); Hayata, *Icon. pl. formos.* **1**: 77 (1911); Matsum., *Index pl. jap.* **2**(2): 364 (1912); H. Léveillé, *Fl. Kouy-Tchéou*: 198 (1914); Sprague in *Curtis's Bot. Mag.* **140**: t. 8557 (1914); Rehder in Sargent, *Pl. wilson.* **2**(2): 402 (1915); House, *Wild fl. New York*: t. 131A (1918–20); R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed., **21**: 176 (1925); Makino & Nemoto, *Fl. Japan*: 540 (1925), 2nd ed.: 747 (1931); Hultén in *Kungl. Svenska Vetenskapsakad. Handl.*, 3rd ser. **8**: 125 (1929); Hand.-Mazz., *Symb. Sin.* **7**: 401 (1931); Komarov & Klob.-Alis., *Opred. r. Dal'nevost kr.* **2**: 748, t. 230, f. 2 (1932); Nakai in *Koryô-sikenrin no Ippan*: 46 (1932); Krylov, *Fl. Zap. Sib.* **8**: 1902 (1935); S. Suzuki in Masamune, *Short fl. Formosa*: 41 (1936); Kitag., *Lin. fl. manshur.*: 317 (1939); Nakai in *J. Jap. Bot.* **18**: 289 (1942); Gorschkova in *Fl. URSS* **15**: 211, t. 9 f. 2 (1949); Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 118, ff. 43, 44 (1951); Grubov, *Konsp. Fl. Mongol. Narod. Respub.*: 205 (1955); Steward, *Man. Vasc. Pls Lower Yangtze Valley China*: 258 (1958); Ohwi, *Fl. Japan*, Engl. ed.: 631 (1965); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 1 (1966); Noda, *Fl. N.-E. Prov. (Manchuria) China*: 793, t. 190 f. 3 (1971); Anon. in *Iconogr. Cormoph. Sinicae* **2**: 875, f. 3479 (1972); N. Robson in *Fl. Taiwan* **2**: 628 (1976), 2nd ed. **2**: 700 (1996); Y. Kimura in *Asahi... shokobutsu*, no. 64: 1509, cum tab. (1977); Liou Tchen-ngo et al. in *Fl. Pl. Herbac. Chinae Bor.-Or.* **6**: 71, t. 27 ff. 1–7 (1977); Kitag., *Neo-lin. fl. manshur.*: 443 (1979); Wu Chingju in *Fl. Intramongolica* **4**: 90, t. 42 ff. 4–7 (1979); Momiyama in Satake et al., *Wild fl.*

Japan **2**: 115, t. 110 (1982); Grubov, *Opred. Sosud. Rast. Mongolii*: 181, t. 97 f. 443 (1982); Hayashi, Azegami & Hishiyama, *Wild fl. Japan*: 358 (1983); Anon. in *Fl. in Desertis R. P. Sinicorum* **2**: 365, t. 130 ff. 1–4 (1987); Wang Jinwu in *Fl. Hebeiensis* **2**: 149, t. 1051 (1988); T. B. Lee, *Ill. Fl. kor.*: 544 (1989); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 43, t. 8 ff. 1–3 (1990); N. Robson in *RHS Dict. Gard.* **2**: 627 (1992), in *Eur. Gdn Fl.* **4**: 58, ff. 9.1, 9.5, 9.9 (1995); Y. N. Lee, *Fl. kor.* 3rd ed.: 230, f. 677 (1998). Type: cult. in Hort. Upsaliensis ex Siberia, *Herb. Linn.* 943.9 (LINN-lectotype, selected here). The Linnaean references to Morison, Wheeler and Ray, and to the Orient, all apply to *H. ascyr*on Mill., which is *H. calycinum* L.

Fig. 9, Maps 3 & 4.

H. fl. pentagynis, caule tetragono (etc.) Gmelin, *Fl. Sibir.* **4**: 178, t. 69 (1769).

Ascyrum tetragonum Moench, *Meth. Bot.*: 130 (1794), nom. illegit. Type as for *H. ascyron* L.

Roscyna gmelinii Spach, *Hist. nat. vég.* Phan. **5**: 430 (1836), in *Ann. Sci. Nat. Bot.* II, **5**: 364 (1836), [*gmelini*], nom. illegit. Type as for *H. ascyron* L.

H. ascyron var. *genuinum* Maxim., *Prim. Fl. amur.*: 65 (1859); in *Bull. Acad. Imp. Sci. Saint- Pétersbourg* **27**: 430 (1882). Type as for *H. ascyron* L.

H. ascyron var. *typicum* R. Keller in *Bot. Jb.* **58**: 191 (1923). Type as for *H. ascyron* L.

Roscyna ascyron (L.) Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 12 (1951), in synon.

Icones: see under infraspecific taxa (pp. 56–58).

Perennial herb 0.5–1.3(–2) mm tall, erect or sometimes ascending from shortly creeping woody base, with stems single or few, caespitose, unbranched or branched above or almost throughout. *Stems* 4-angled when young, becoming 4-lined or occasionally internodes 2-lined below; internodes 2–12 mm, exceeding leaves or shorter than them. *Leaves* sessile; lamina (30–)40–97(–120) × (4–)7–35(–40) mm ovate-lanceolate or ± narrowly lanceolate or narrowly oblong or narrowly elliptic to oblong-linear or oblanceolate, rather paler beneath, not glaucous, plane, chartaceous; apex acute to subapiculate or obtuse (or lowermost rarely rounded), margin entire, base cuneate to cordate-amplexicaul; venation: 4–7 pairs of main laterals from lower half of midrib, with subsidiary midrib branches and dense tertiary reticulation not prominent, often obscure; laminar glands pale, dense, unequal dots or short streaks; intramarginal glands pale, small, dense. *Inflorescence* 1–*c.* 35-flowered from 1–5 nodes, the whole subcorymbiform to narrowly pyramidal, sometimes with flowering branches from up to 4 nodes below; pedicels 5–30 mm in fruit; bracts and bracteoles foliar but smaller and often broader, more rarely linear-lanceolate and deciduous. *Flowers* 30–70(–80) mm in diam., stellate with petals spreading to reflexed; buds broadly to narrowly ovoid, rounded to subacute. *Sepals* (3–)5–15 × (1.5–)2–7(–10) mm, free, imbricate, subequal to unequal, the outer ones sometimes foliaceous, erect in bud and fruit, oblong to elliptic or ovate to ovate–lanceolate or obovate, rounded to obtuse or more rarely subacuminate to acute, entire; veins *c.* 11–17, branching and uniting distally, midrib scarcely differentiated; laminar glands linear, distally interrupted to striiform; marginal glands spaced, small. *Petals* bright (to golden?) yellow, sometimes tinged red in bud, 14–41 × 5–20 mm, 2–3 × sepals or relatively shorter when sepals foliaceous, obovate or oblong-obovate to oblanceolate, often somewhat spathulate to subunguiculate, strongly curved to almost straight, rounded or obtuse to rarely acute or acuminate, with apiculus short and rounded or absent, margin entire; laminar glands pale, linear to distally striiform, or absent; marginal glands absent. *Stamen fascicles* 5(4?), distally red, each with *c.* 30 stamens, longest 9–25 mm, *c.* 0.4–0.67 × petals; anther reddish, gland amber. *Ovary* 5(4)-locular, 4–7(–9) × 3–5 mm, broadly ovoid to narrowly ovoid-pyramidal or ellipsoid; styles 5(4), 2.5–15 mm, *c.* 0.5–2 × ovary, free or up to 0.8 coherent or connate; stigmas broadly capitate to infundibuliform. *Capsule* 9–22(–30) × 5–13 mm, broadly to narrowly ovoid or ovoid-pyramidal or rarely narrowly cylindric, 2–3 × sepals, obtuse to rounded, with numerous narrow longitudinal vittae. *Seeds* dark red-brown, 1–1.5 mm, cylindric, not or slightly curved, deeply carinate or narrowly winged, sometimes with slight terminal expansion; testa densely shallowly linear-reticulate. 2n = *c.* 22–20 (Krasnoborov et al., 1980), 18 (Kogi, 1984; Malakhova, 1990; Nishikawa, 1990; Malakhova & Markova, 1994; Stepanov, 1994; '*H. gebleri*' n = 9, Nielsen, 1924), 16 (Krogulevich, 1978).

Moist to dry meadows or grassy or rocky slopes, sometimes in forest or amongst scrub, streamsides and river banks; 0–2800(–3600) m.

Russian Federation (Altai to Kamchatka and Kurile Is., Sakhalin), Mongolia, Korea, Japan, Taiwan, China (all provinces except Xizang and Qinghai), Vietnam (north); Canada (Quebec, Ontario, Manitoba?), U.S.A. (Minnesota to Vermont and south to Missouri, Illinois and Maryland).

H. ascyron is a highly polymorphic species or species complex with a very wide distribution. Although several varieties or even species have been recognized, the variation appears to be almost continuous. Seven characters or character groups appear to vary independently or with insufficient correlation or disjunction to be useful for specific delimitation:

(1) Habit/inflorescence: from (a) simple, unbranched, 3-flowered to (b) pyramidally branched with flowers on each branch or (c) widely corymbiform ('var. *umbellatum*').
(2) Leaves: from (a) large, triangular-lanceolate, acute to (b) small, narrowly oblong to linear, acute or (c) oblong, obtuse to (upper) very rarely almost rounded or (d) rather broadly elliptic and subacute ('*H. hemsleyanum*') to almost rounded.
(3) Flowers: from large to small, varying approximately with (1) and (2) except for (a) an extra-large-flowered form with long, mostly united styles ('var. *longistylum*' in part) and (b) Manchurian plants with large flowers and small leaves.
(4) Sepals: from (a) oblong or oblong-elliptic, rounded to (b) narrowly oblong, rounded (subsp. *gebleri*) or (c) ovate, acute (subsp. *pyramidatum*) or (d) obovate to foliaceous, rounded (var. *macrosepalum*) or (e) ovate-lanceolate.
(5) Styles: from (a) medium long and up to 0.75 united to (b) long, *c.* 0.8 connate (see (3) above) or (c) shorter than ovary and free (mostly subsp. *gebleri*). (5) varies with (4) in general but not completely. Some small-flowered, small-leaved plants from south China and Japan ('forma *angustifolium*') have styles about half connate, while some large-flowered plants with broad sepals have short, free styles (Nei Mongol).
(6) Capsules: from (a) large ovoid-pyramidal to (b) small ovoid-cylindric (subsp. *gebleri*) or (c) narrowly cylindric ('var. *giraldii*').
(7) In addition, the pedicels vary in length from *c.* 10 mm to (a) 30 mm or (b) *c.* 5 mm ('var. *umbellatum*').

The most frequently distinguished taxon has been *H. gebleri* Ledeb., which most Russian authors have recognized, as it occurs through southern Siberia from Altai to the Korean border along with distinct larger-flowered less-branched forms and is present alone in Kamchatka, the Kuriles and Sakhalin. On the other hand, Chinese

authors have tended to include it in *H. ascyron*, because intermediate forms occur in the north of that country.

The North American plants were early recognized at species level (*H. pyramidatum*, *H. macrocarpum*, etc.) and Kimura (1951) maintained them as var. *americanum* partly on the basis of their rather acute sepals. Already in 1882, however, Maximowicz (1882: 163) and slightly later Coulter (1886: 83) had expressed the opinion that they could not be distinguished from the Asian plants by this or any of the other differentiating characters that had been proposed. I can confirm that two of Kimura's other characters – leaf shape and styles shortly connate – do not help to define a discrete taxon. The American plants, however, all have short styles and most have somewhat acute sepals, a combination that does not occur elsewhere in the species. Kimura's other varieties were based mainly on these style length and union criteria: var. *longistylum* with styles up to 15 mm, 2/3 to 3/4 united, var. *ascyron* with styles up to 7 mm, 1/3 to 2/3 united (both with styles equal to or longer than the ovary), and var. *brevistylum* with styles shorter than the ovary and free.

In these circumstances it seems best to distinguish the northern Asian *H. gebleri* and the North American *H. pyramidatum* as subspecies (although further investigation may show that the intermediate forms in the former are too numerous to maintain it even at this rank). It seems impossible to recognize the long-styled (mainly large-flowered and northern) plants and the narrow-fruited central Chinese ones (respectively vars *longistylum* and *giraldii* (≈ var. *hupehensis*)) as distinct taxa, as both represent extremes of continuous variation. Likewise, the narrow-leaved small-flowered form from south China (wrongly identified by me and others as var. *angustifolium* Y. Kimura) merges with more typical forms.

1a. **Hypericum ascyron** subsp. **ascyron**
Fig. 9A, Map 3.

Ascyrum sibiricum Lam. ex Poiret, *Tabl. encycl.* **3**: 200, t. 642 (1823). Type as for *H. ascyron* L.

?H. salicaria Rchb., *Iconogr. Bot.*, cent. 5: 53, t. 490, f. 183 (1827). Type: cult. ex Kazakhstan, 'ad Noor-Saisan in mont. Alt.', *L[edebour]* s.n. (W?-holotype). See note under subsp. *gebleri*.

H. ascyron var. *macrosepalum* Ledeb., *Fl. altaic.* **3**: 364 (1831), *Fl. ross.* **1**: 446 (1842); Krylov, *Fl. Altaya*: 189 (1901), *Fl. Zap. Sib.* **8**: 1903 (1935). Type: Russian Federation, W. Siberia, Altayskiy Kray, 'prope pagum Uimon ad fl. Katunja'. *B[unge]* (LE).

Roscyna japonica Blume, *Mus. bot.* **2**: 21 (1856). Type: Japan, *Herb. von Siebold* (L-holotype).

H. ascyron var. [β] *longistylum* Maxim., *Prim. fl. amur.*: 65 (1859), in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 430 (1882), *Mél. Biol.* **11**: 162 (1882); Palibin, *Consp. fl. Koreae* **1**: 44 (1898); H. Léveillé in *Bull. Soc. Bot. France* **53**: 499 (1906); Nakai in *J. Coll. Sci. Imp. Univ. Tokyo* **26**: 96 (1909) [*Fl. Korea*], *Tyôsen-syokubutu* **1**: 159, f. 190 (1914); Matsum., *Index pl. jap.* **2**: 364 (1912); Koidz., *Fl. Symb. Orient.-Asiat.*: 91 (1930) pro syn. *H. sagittifolii* ut forma; Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 125, f. 44C (1951); Ohwi, *Fl. Japan*, Engl. ed.: 631 (1965); Liou Tchen-ngo et al. in *Fl. pls. Herbac. Chinae Bor.-Or.* **6**: 71, t. 27 f. 8 (1977); Kitag., *Neo-lin. fl. manshur.*: 443 (1979); Y. N. Lee, *Fl. kor.* 3rd ed.: 230, f. 678 (1998). Type: Russian Federation (east Siberia), Chöchzier ad Amurem non procul ab Ussuri ostio, *Maximowicz* s.n. (LE-holotype).

H. ascyron var. *micropetalum* R. Keller in *Bull. Herb. Boiss.* **5**: 638 (1897) ['forma *micropetalum* var. nov.'], in *Bot. Jb.* **33**: 550 (1904) pro parte excl. specim. cit., in *Bot. Jb.* **58**: 191 (1923); H. Léveillé in *Bull. Soc. Bot. France* **53**: 499 (1906), op. cit. **54**: 592 (1908) pro parte excl. specim. cit.; Matsum., *Index pl. jap.* **2**: 364 (1912); Makino & Nemoto, *Fl. Japan*: 540 (1925), 2nd ed.: 747 (1931). Type: Japan, in planitie Sambingi, *Faurie* 1885 (Z-lectotype, selected here); prope Nuruyu, *Faurie* 793 (Z-syntype).

H. longifolium H. Léveillé in *Bull. Soc. Agric. Sarthe* **39**: 322 (1904), in *Bull. Soc. Bot. France.* **54**: 590 (1908), in *Repert. Spec. Nov. Regni Veg.* **6**: 375 (1909), *Fl. Kouy-Tchéou*: 199 (1914) pro parte quoad *Esquirol* 1461; Rehder in *J. Arnold Arbor.* **15**: 191 (1934). Type: China, Guizhou, près Ke-ma-tong, mont. du Collège, 9 August 1897 (fl & fr), *Bodinier* 1774 (E!-holotype).

H. scallanii R. Keller in *Bot. Jb.* **33**: 549 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 590 (1908), in *Fl. Kouy-Tchéou*: 199 (1914). Type: China, Sichuan, in monte Uo-mi-san [Emei shan] prope Tcen-to-sen, September 1899 (fl), *Scallan* in *Biondi* 3808 (FI!-holotype).

H. ascyron var. *giraldii* R. Keller in *Bot. Jb.* **33**: 550 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 592 (1908). Type: China, Shaanxi (all), in alto monte Huan-tou-san, July 1889 (fl), *Giraldi* in *Biondi* 3805 (FI!-lectotype selected here); in rupestribus montis Kian-san prope Sce-kin-tsuen, 4 August 1897 (fl), *Giraldi* in *Biondi* 3803 (FI!-syntype); Lao-y-san, Thin-kio-tsuen, July 1899 (fl), *Giraldi* in *Biondi* 3804 (FI!-syntype); in occidentem montis Ngo-san, August 1899 (fl), *Giraldi* in *Biondi* 3806 (FI!-syntype); in monte Uo-mi-san prope Tcen-to-san, *Scallan* in *Biondi* 3807 (FI!-syntype).

H. biondii R. Keller in *Bot. Jb.* **33**: 551 (1904) pro parte quoad lectotypus. Type: China, Shaanxi, Monte di Mang-hua-san ad ovest di Si-ngan-fu e distante tre giornale, October–November 1894 (fr), *Giraldi* in *Biondi* 530 (FI!-lectotype, selected here); in monte Thae-pei-san, September [1894?], *Giraldi* 529 (FI-syntype).

H. ascyron var. *umbellatum* R. Keller in *Bot. Jb.* **33**: 550 (1904). Type: China, Shaanxi, Ki-san, 1896 (fr), *Scallan* in *Biondi* 3813 (FI!-holotype).

H. ascyron [var.] *macropetalum* hort. ex Vilmorin & D. Bois., *Fruct. Vilmor.*: 24 (1904), nomen.

H. kelleri H. Léveillé in *Bull. Soc. Bot. France* **54**: 499 (1906) [et in clav. p. 497, qua 'Lévl. & Vant.'], non Baldacci (1895). Type: Japan [without precise locality], *Faurie* s.n. (P-holotype). Apart from having only 4 styles, this plant (as described) would appear to be typical *H. ascyron*.

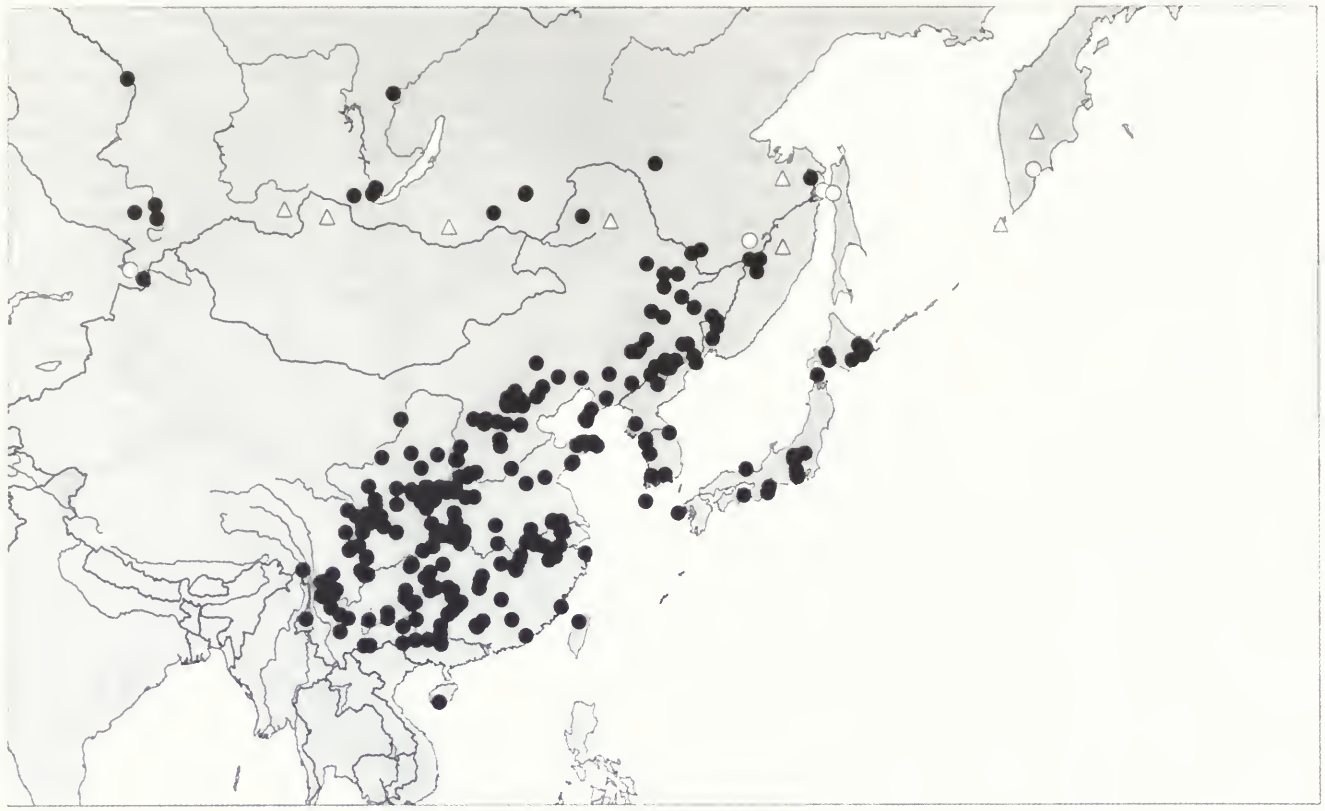
H. yabei H. Léveillé & Vaniot in *Repert. Spec. Nov. Regni Veg.* **5**: 279 (1908) non H. Léveillé & Vaniot in *Bull. Soc. Bot. France* **53**: 501 (1906); Nakai in *J. Coll. Sci. Imp. Univ. Tokyo* **31**: 453 (1911). Type: Korea, Quelpaert I., August 1907, *Faurie* 1792 (E!-holotype).

H. hemsleyanum H. Léveillé & Vaniot in *Bull. Soc. Bot. France* **54**: 592 (1908), in *Mem. Real. Acad. Ci. Barcelona* III, **12**: 553 (1916); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 3 (1966). Type: China, Jiangsu, Zuo-se, n.d. (fl.), *d'Argy* s.n. (E!-holotype; BM!-isotype).

H. ascyron var. *hupehensis* Pamp. in *Nuov. Giorn. Bot. Ital.* N.S. **17**: 669 (1911), op. cit. N.S. **18**: 129 (1911). Type: China, Hubei, 14 syntypes from southern mountains at 600–1850 m, *Silvestri* 1471–1481 + 1471a, 1472a, 1479a (all FI); Monte Cia-inen-ku presjo Sian-yang, *Silvestri* 1471 (FI-lectotype, A!, photo, is selected here). This variety is very like var. *giraldii*, but differs in that the leaves are not or scarcely cordate, the flowers are larger (40–50 mm in diam.) and the capsule is shorter (8–10 mm wide).

H. ascyron var. *vilmorinii* Rehder in *Mitt. Deutsch. Dendrol. Ges.* **24**: 235 (1916), in Bailey, *Stand. Cyclop. Hort.* **3**: 1630 (1919). Type: cf. Sprague in *Curtis's Bot. Mag.*: t. 8557 (1914) as *H. ascyron*. This appears to be a re-naming of *H. ascyron* var. *macropetalum* (1904).

Fig. 9 A. *H. ascyron* subsp. *ascyron*: (a) habit (medium-styled); (b) long-styled ovary; (c) medium-styled ovary; (d) medium-styled capsule. B. *H. ascyron* subsp. *pyramidatum*: (e) capsule. C: *H. ascyron* subsp. *gebleri*: (f) leaf; (g) capsule. D. *H. concinnum*: (h) habit; (i) capsule (a, f, g, h × 1; rest × 3). A. *Bisset* 3465, except (b) *Chen* 199. B. *Burgess* 343. C. Redrawn from Ledebour, *Ic. fl. ross.*: t. 487. D. (h) *Krautter* s. n.; (i) *Meebold* 9798.



Map 3 Sect. 7: 1a. *H. ascyron* subsp. *ascyron* ●; 1b. *H. ascyron* subsp. *gebleri* ○ specimens, other records Δ.

H. ascyron var. *adamii* R. Keller in *Bot. Jb.*: **58**: 191 (1923). Type: Japan or Korea, *Warburg* s.n. (B†-holotype).

H. sagittifolium Koidz., *Fl. symb. orient.-asiat.*: 91 (1930). Type as for *H. yabei* H. Léveillé & Vaniot (1908 non 1906). '*H. ascyron* f. *longistylum* Maxim.' is also cited.

H. ascyron forma *vilmorinii* (Rehder) Rehder, *Bibl. cult. trees* : 462 (1949).

H. ascyron var. *ascyron* f. *angustifolium* Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 125 (1951). Type: Japan, Honshu, Prov. Kai [Yamanashi], Yamanaka, 29 July 1934, *Y. Kimura* 3486 (TI-holotype).

Icones: Rchb., *Iconogr. Bot.*, cent. 5: t. 490, f. 183 (1827); Sprague in *Curtis's Bot. Mag.*: t. 8557 (1914); Liou Tchen-ngo et al. in *Fl. Pl. Herbac. Chinae Bor.-Or.* **6**: 71, t. 27 ff. 1–7 (1977).

Plant 0.5–1.3m tall. *Leaves* 40–120 × (5–)7–40 mm, ovate-lanceolate or rarely narrowly elliptic to linear-lanceolate or narrowly oblong, base usually cordate-amplexicaul. *Flowers* 45–80 mm in diam. *Sepals* 6–10 mm wide, ovate or oblong to elliptic or lanceolate or obovate, rounded to obtuse or rarely apiculate to acute. *Styles* 4–15 mm, almost free to up to 0.8 united. *Capsule* ovoid to ovoid-pyramidal or ovoid-cylindric.

Distribution of the species (see p. 53), except for north-west and north-east China (Xinjiang, north Manchuria), Sakhalin, Kamchatka, the Kurile Is. and North America.

RUSSIAN FEDERATION. Ob: ad ripas fl. Ob prope Bogorodskoje, 29 June 1892 (fl), 30 August 1892 (fr), *Krylov* 1918 (H). **Irtysh**: (Gorschkova, 1949). **Altai**: Altai, pre-1893 (fl), *Thomas* in Herb. Boiss. (G); Gorno-Altaiskaya Avt. Obl., Elekmonarskiy raion, okrestnosti sela Chemal u ruchya, 29 August? 1961, *Velikanov* s.n. (H). **Angara-Sayan**: Irkutzk, 1874 (fl), *Augustinowicz* s.n. (K, LE*); Transbaikalia, montis Arschan, 12–16 July 1911 (fl), *Ahuger* s.n. (H); Reg. transbaical., ad pagum Verchne-Ubukunsk (juxta flumen Selenga), 500–1000 m, 20 July 1900 (fl), *Ehrenberg* s.n. (H). **Dauria**: Nerchinsk, Schilkafluss, bei Monastyr, 1892 (fl & fr), *Karo* 220 (E, H); Juzhn. Zabaykalskiy, Khentai-Gukonskoye nagorye, Bas. r. Gukoi, 18 August 1960 (fl), *Maksimova* s.n. (K, LE*). **Zeya-Bureya**: Zejskaja Pristán am Zeaflusse, July 1899 (fl), *Karo* 377 (BM, E, G*, H, JE). **Uda**: Khabarovskii krai, Ul'chskii raion 1 km E. of Susanino, road to Anninskie Vody, 40 m, 27 August 1976 (fr), *Alanko* (H). **Ussuri**: Prov. Amurensis, fluvium Amur vallis Uril, in pratis inter Uril et Yrjasnaja, 5 July 1895 (fl), *Komarov* 1090 (BM, K); Prov. Amur. in monte Hehzier prope stationem ferrosam Korfowskaja, circa a 40 km procul ab oppido Chabarowsk, 3 August 1913, *Enander* s.n. (E).

MONGOLIA. Khentei, Khangai, Mongol-Daurian and Great Khingan regions (Grubanov, 1996).

CHINA. Nei Mongol: Ningcheng Xian, Cunjingou Gongshe, 21 July 1981 (fl), *Li* S.X. et al. 4438 (IFP). **Heilongjiang**: Khalka Gol, 27 July 1902 (fl), *Campbell* s.n. (BM); Daishan, 20 July 1956 (fl), *Zhongde Exped.* 7614 (PE). **Jilin**: Districtus Omoso, Trajectus Tien-guan-czai-lin, 12 August 1896 (fl & fr), *Komarov* 1091 (BM); Zhangjiadian, 26 July 1958 (fl), *Wang* C.S. et al. 1512 (IBSC). **Liaoning**: Dairen [Talien], June–August 1910 (fl), *Stuart* s.n. (BM); Huanren, 23 August 1964 (fr), *Cui & Zhu* 186 (PE). **Hebei**: Tche-ly, montagnes du Fou-Ping, August 1910 (fr), *Chanet* 542 (BM, E); Tong Ling, 7 July 1935 (fl), *Liu Y.* 11606 (IBSC). **Shanxi**: Qin Xian, Wulongchuan, 16 July 1959 (fl), *Chen Y.L.* 899 (PE); Lishan Xian?, Muchang Gou, 1550 m, 29 June 1955 (fl), *Huanghe Exped.* 2288 (PE). **Shaanxi**: Shensi Central, voyage à Cheu hai yao, 1100 m, 13 August 1916 (fr), *Licent* 2438 (BM, K); Liuba Xian, Miaotaizi, 1500 m, 6 September 1977 (fr), *Wang & Shi* 308 (PE). **Gansu**: Lien hoa shan, Ha Kai valley, 2700 m, 14–20 July 1925 (fl), *Rock* 12772 (E, GH, K); Heshui Xian, Taibai Zhen, 1250 m, 17 July 1954, *Huanghe Exped.* 606 (IBSC, PE). **Ningxia**: Jingyuan Xian, Danan Chuan, Nantai Gou, 2300 m, 28 July 1964 (fl), *Jingyuan Exped.* 36 (PE). **Henan**: Lushi Xian, 1180 m, 28 September 1958 (fr), *Fu J.Q.* 1446 (IBSC); Lushih-hsien, Hsuingerhling, 12 July 1935 (fl), *Liou* 4712 (K). **Shandong**: Fei Hsien, Meng Shan, 700m, 29 July 1936 (fr), *Cheo & Yen* 241 (BM); Lao Shan, 600 m, 1 July 1930 (fl), *Chiao C.Y.* 2658 (GH, IBSC, NY); behind Fu Shan, 150 m, 7 July 1923 (fl), *Sha F.H.* 169 (PE).

Jiangsu: Nanking, 21 July 1922 (fl), *Yu P.L.* in *Herb. Univ. Nanking* 2999 (E); Yixing Xian, Longchi Shan, 25 June 1962 (fl), *Mao S.H. et al.* 71 (KUH, NAS). **Anhui**: Yang chia ping, July 1905 (fl), *Schindler* 39 (BM, E, K); Taiping, Longyuan, 23 June 1959 (fl), *Anhui Exped.* 600 (IBSC). **Zhejiang**: Ningpo, 1874 (fl), *Forbes* 1081 (BM); Tianmu Shan, 15 July 1957 (fl), *He X.Y.* 25408 (IBSC). **Fujian**: Diongloh, Sin Sai, 24 July 1925 (fl), *Cheng P.E.* 2407 (BO). **Jiangxi**: Lu Shan, n.d. (fr), *Hsiung Y.K.* 6928 (IBSC); Xunwu Xian, Jingxi Gonshe, 700 m, 13 August 1962 (fr), *Yue J.S.* et al. 1824 (KUN). **Guangdong**: Yangshan Xian, S. of Linchow, July–September 1932 (fr), *Tsui T.M.* 580 (GH, K, NY, PE); Chaoan Xian, 25 April 1973 (fr), *Luo X.R.* 1297 (IBSC). **Hainan**: Chahar, Hsiao-wu-tai-shan Exped., 6 July 1936 (fl), *Wu & Yang* 36810 (PE). **Guangxi**: Nandan Xian, Mangchang, Jiuwei Shan, 2500 m, 3 July 1937 (fl), *Wang C.* 40964 (A, IBSC); Gui Xian, Tan Tang, 4 October 1958 (st), *Zhong S.Q.* 21098 (KUN). **Hunan**: prope urbem Wukang, 350–1400 m, 4 June–9 August 1918, *Handel-Mazzetti* 12270 (E); Qianyang Xian, 28 June 1954 (fl), *Lee C.T.* 2487 (IBSC, PE). **Hubei**: Hsing Shan, June 1901 (fl), *Wilson* 2200 (E, K); Wuchang, Luojiashan, 6 September 1932, *Chung H.H.* 9177 (A); Lichuan Xian, 1500 m, 24 September 1951, *Dai & Qian* 1541 (PE). **Sichuan**: Jiuzhaigou, NW of Songpan, 3000 m, 10 September 1986 (fl), *Lancaster* 1602 (BM); Mu-li hsien, 2450 m, 19 August 1978 (fr), *Zhao* C.S. et al. 7574 (SZ). **Guizhou**: Yanhe Xian, Daping, 1000 m, 22 July 1957 (fl), *N. Guizhou (Qianbei) Exped.* 2416 (PE); Ya-Tze-Ho, Tsingchen, 5 July 1935 (fl), *Teng S.W.* 762 (IBSC). **Yunnan**: Mo-so-yan, près de Lan Kong, 5 August 1883 (fl & fr), *Delavay* 111 (P); Pingbian Xian, 1300 m, 20 July 1934 (fl), *Tsai H.T.* 61036 (A, IBSC, NAS, PE); Chungtien [Zhongdian], Haba, 2600 m, 25 November 1937 (fr), *Yu, T.T* 14964 (KUN). **Qinghai**: no precise locality, 1901 (fl), *Zimmermann* 229 (US).

VIETNAM. Indo-China, July 1924 (fl), *Petelot* s.n. (BO).

TAIWAN. Hsinchu: Sintiku, 18 May 1923 (fl), *Simada* 1209C (TAI).

KOREA. North: 80 km from Seoul, Wusan and Pyongyang [3 localities], 1892 (fl), *Veitch* 56 (BM). **South**: Chemulpo, July 1884 (fl), *Carles* 105 (BM, E, K); Kang Wong Prov., Inje Distr., Sorak-san Nat. Park, road to Paekdamsa Temple, 450 m, 28 September 1989, *Kirkham, Flanagan & Boyce* KFBX 26 (K); in Chinnampo, August 1906 (fl), *Faurie* 635 (E); Port Chusan [Ullungdo I.], June 1859 (fl), *Wilford* 928 (K); Quelpaert [Cheju], in herbidis Hoakin, August 1909 (fl), *Taquet* 1678 (E, K).

JAPAN. Hokkaidô. Oshima: Yezo, in planitie Hakodate, August 1905 (fl), *Faurie* 6902 (BM); Hakodate, 1861 (fl & e. fr), *Maximowicz* Iter II s.n. (BM, K). **Shirabeshi**: Mt. Moiwa, August 1912 (fl & fr), *Sakamura* in *Kudo* 1254 (TAI). **Iburi**: Tomokomai Forest, 31 August 1914 (fl & fr), *Yoshimi* in *Kudo* 121 (TAI). **Ishikari**: Sapporo, 29 July 1991 (e. fr), *Tokobuchi* s.n. (K). **Kushiro**: Me-akan dake, 2 August 1929 (fl), *Tanaka* 164 (BM); Nita Teshikaga-Chô, 5 August 1974 (fl), *Furuse* 6660 (K). **Honshû. Tochigi**: Nikko-Chuzugi in Shimotsuko, 7 September 1952 (fr), *Kubota* NSM 695 (BM, E, H, K). **Gunma**: Mt. Akagi, 11 July 1949 (fl), *Tanaka* s.n. (K); Chusenji[-ko], August 1887 (l. fl), *Bisset* 4269 (BM, E). **Nagano**: Karuizawa, 1050 m, 3 August 1912 (fl), *Fox* s.n. (BM). **Tokyo**: Komaba, 26 October 1878 (fr), *Bisset* 1472 (E); Musashi, Akabane, 10 August 1910 *Sakurai* s.n. (H). **Kanagawa**: Lagami, Mt. Hakone, August 1906, *Yokohama Nursery Co.* s.n. (E). **Shizuoka**: Prov. Kai, Minamitsuru-gun, Mt. Fuji, 1933 (fl & e. fr), *Makino* 7697 (CAS, E). **Mie**: Ise, Nago, August 1907 (fl & fr), *Yokohama Nursery Co.* s.n. (E). **Nara**: Mt. Izawa, 8 September 1941 (fr), *Seki* in HTU 77587 (TAI). **Shikoku. Tokoshima**: Kumatani, 1914 (fl), *Takayanagi* in *Sasaki* HTU 76870 (TAI). **Kyûshû. Nagasaki**: Nagasaki, Kundshovan, 1863 (fr), *Maximowicz* Iter II s.n. (K).

CULTIVATED. Specimens seen from England (1763→), Scotland (1827–1898), Ireland (1968), France (1841), Belgium (1979), Sweden (18th C) and Finland (1911–1978).

1b. **Hypericum ascyron** subsp. **gebleri** (Ledeb.) N. Robson, **stat. nov.** Type as for *H. gebleri* Ledeb.

Fig. 9C, Map 3.

Hypericum gebleri Ledeb., *Fl. altaic.* **3**: 364 (1831), *Icon. pl.*: 487 (1834), *Fl. ross.* **1**: 446 (1842); Maxim.; *Primit. fl. amur.*: 461 (1859), in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 431 (1882), *Mél. Biol.* **11**: 163 (1882); Krylov, *Fl. Altaya*: 189 (1901); Komarov, *Fl. Manshur.* **3**: 42 (1905); H. Léveillé in *Bull. Soc. Bot. France* **54**: 593 (1908); Nakai, *Tyosen-syokubutu* **1**: 158, f. 189 (1914), *Fl. Mt. Paik-tu san*: 67 (1917); Miyabe & Miyake, *Fl. Saghalin*: 78 (1915); Kudo in *J. Agric. Hokkaido Univ.* **12**: 47 (1923); ? in *Kitabahuto-Syokobutu-Tyôsyo*: 179, t. 17, f. 85 (1924); Makino & Nemoto, *Fl. Jap.*: 541 (1925); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 176 (1925); Komarov, *Fl. pol. Kamch.* **2**: 303 (1929); Hultén in *Kungl. Svenska Vetenskapsakad Handl.*, 3rd ser. **8**: 126, map 554 (1929); Komarov & Kleb.-Alis., *Opred. r. Dal'nevost kr.* **2**: 748 (1932); Krylov, *Fl. Zap. Sib.* **8**: 1903 (1935); Sugawara, *Ill. fl. Saghalien* **3**: 1301, t. 598 (1940), repr. (1975); Gorschkova in *Fl. URSS* **15**: 213 (1949); Grubov, *Konsp. Fl. Mongol. Narod. Respub.*: 205 (1955), *Opred. Sosu. Rast. Mongolii*: 181 (1982); Pavlov et al., *Fl. Khazakhstana* **6**: 161 (1963); Noda, *Fl. N.-E. Prov. (Manchuria) of China*: 794 (1971); Liou Tchen-ngo et al. in *Fl. Pl. Herbac. Chinae Bor.-Or.* **6**: 73, t. 27, ff. 9–12 (1977). Type: Kazakhstan, Altai, 'Habitat ad montium latera juxta fl. Buchtarma ex adverso Sinensium praesidii Dschingis-tei', July–August (fl), *Ledebour* s.n. (LE-holotype).

Roscyna gebleri (Ledeb.) Spach, *Hist. nat. vég.* Phan. **5**: 430 (1836), in *Annls Sci. Nat. Bot.* II, **5**: 64 (1836).

H. ascyron var. *brevistylum* Maxim., *Primit. fl. amur.*: 65 (1859); H. Léveillé in *Bull. Soc. Bot. France.* **53**: 498 (1906); Kitag., *Neo-lin. fl. manshur.*: 443 (1979). Type: Russian Federation, E. Siberia, prope Dshai, 50 circa stadia a pago Kitsi, *Maack* s.n. (LE-syntype); infra montes Burejae, *Maack* s.n. (LE-syntype). Maximowicz (loc cit. above) stated that this plant was *H. gebleri* Ledeb. unless the narrowly ovate-oblong leaves made it different; by 1882 (*Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 431) he had decided to include it in that species.

H. sachalinense H. Léveillé in *Repert. Spec. Nov. Regni Veg.* **6**: 330 (1909); Gorschkova in *Fl. URSS* **15**: 257 (1949). Type: Russia, E. Siberia, Sakhalin I., Vladimirov, August 1908 (fl), *Faurie* 518 (E!-lectotype, selected here; BM!, W!–syntypes); Vladimirov, September 1908 (fr), *Faurie* 519 (BM!, E!, W!-syntypes); Saghalien, September 1908 (fr), *Faurie* s.n. (E!-syntype).

Icones: Ledeb., *Icon. fl. ross.* **5**: t. 487 (1834); Suguwara, *Ill. fl. Saghalien* **3**: 1300, t. 598 (1940).

Plant 0.5–1 m tall. *Leaves* 30–60 × 4–15 mm, narrowly lanceolate or narrowly elliptic-lanceolate to oblong-linear or oblanceolate, base usually cuneate. *Flowers* 45–50 mm in diam. *Sepals* 1.5–7 mm wide, narrowly oblong or oblong-lanceolate, rounded or usually obtuse to acute. *Styles c.* 2.5–3.5 mm, about half as long as ovary, free. *Capsule* cylindric-ellipsoid.

Kazakhstan, Russia (Altai, Angara-Sayan, Dauria, Zeya-Bureya, Uda, Ussuri, Sakhalin, northern Kurile Is., Kamchatka), Mongolia, China (extreme west Xinjiang, Heilongjiang, Jilin?), Korea (north).

KAZAKHSTAN. Altai: Songaria chin., ad lacum Saisang-Nor, 1838 (fl), [*Fischer*] s.n. (K, LE*).

RUSSIAN FEDERATION. Angara-Sayan and **Dauria** (Gorschkova, 1949). **Zeya-Bureya**: Amur, 1871 (fl), *Augustinowicz* s.n. (K, LE*). **Uda**: Bureinskiy Khrebet, infra montes Burejae, *Maack* s.n. (LE*). **Ussuri**: (Gorschkova, 1949). **Sakhalin**: Vladimirov, August 1908 (fl), *Faurie* 518 (BM, E, W). **Kamchatka**: Kamtchatka australis, Savoiko, 27 July 1928 (fl), *Eyerdam* s.n. (E), *Malaise* s.n. (K); Kimitina R., 50 km NW from Mashura (Hultén, 1929). **Kurile Islands**: no locality cited (Gorschkova, 1949).

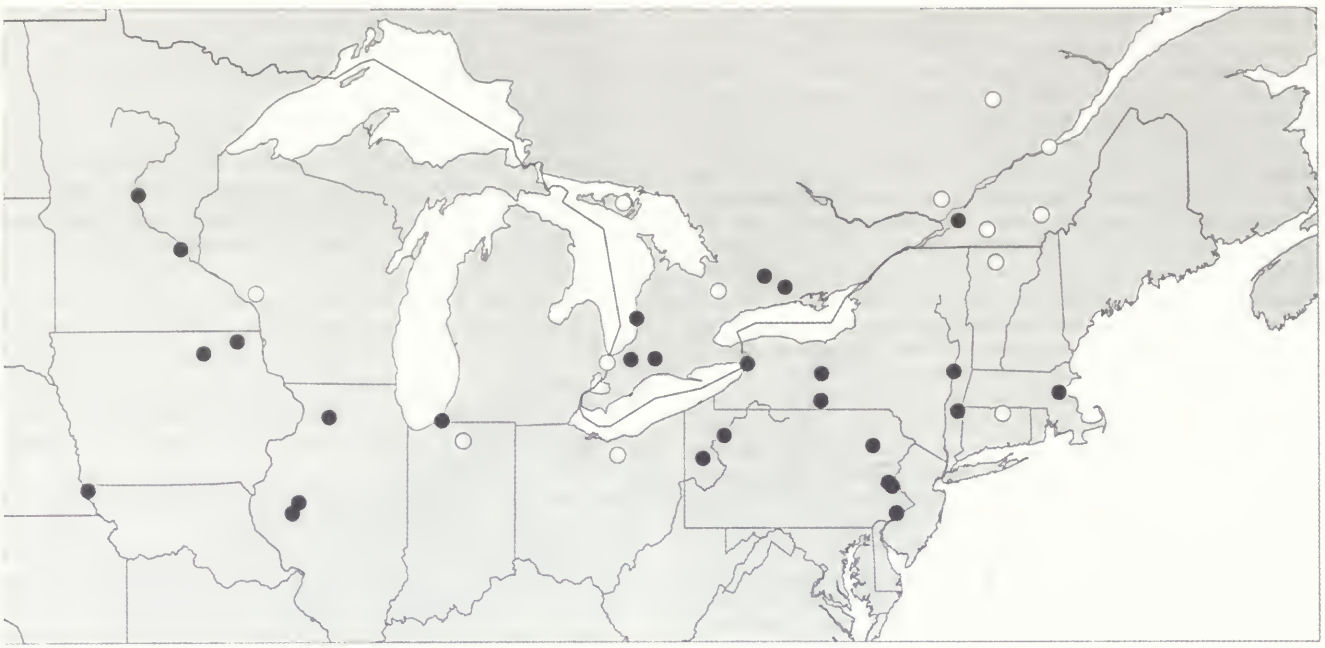
MONGOLIA. Khentei (Grubanov, 1996).

CHINA. Heilongjiang, Jilin? (Komarov, 1950).

KOREA. North: via ab oppido Musang ad oppidum Kapsan, Vallis Tadin-don, 22 June 1897 (fl), *Komarov* 1091 (K).

When making a survey of Chinese specimens in 1993, I had not then decided to recognize subspecies in *H. ascyron.* I do not, therefore, have detailed records of the occurrence of subsp. *gebleri* in the north of China.

Reichenbach's illustration of *H. salicaria* (see synonymy of



Map 4 Sect. 7: 1c. *H. ascyron* subsp. *pyramidatum* ● specimens, ○ other records.

subsp. *ascyron*) shows a plant with narrow leaves basally rounded and small flowers with narrow but unequal foliaceous sepals, short free styles and a pyramidally ovoid capsule. If this apparent intermediate form between subsp. *ascyron* and subsp. *gebleri* has arisen independently of the Chinese intermediates, then subsp. *gebleri* would be diphyletic in origin. The epithet *gebleri* would then go with the Altai plant.

1c. **Hypericum ascyron** subsp. **pyramidatum** (Aiton) N. Robson, **comb. et stat. nov.** Type as for *H. pyramidatum* Aiton.

Fig. 9B, Map 4.

H. bartramium Miller, *Gard. Dict.* 8th ed., no. 10 (1768). Type: Cult. ex America in Hort. Chelsea (BM!-holotype).

H. pyramidatum Aiton, *Hort. kew.* **3**: 103 (1789), op. cit., 2nd ed. **4**: 422 (1812); Willd, *Sp. pl.* **3**: 1444 (1802); Vent., *Jard. Malmaison* **2**: t. 118 (1804); Pursh, *Fl. Amer. sept.*: 374 (1814); Choisy, *Prodr. monogr. Hypéric.*: 41 (1821), in DC., *Prodr.* **1**: 544 (1824); Sprengel, *Syst. veg.* **3**: 342 (1826); Torrey & Gray, *Fl. N. Am.* **1**: 158 (1838); Gleason, *New Britton & Brown Ill. Fl.* **2**: 541 (1952); Steyerm., *Fl. Missouri*: 1058 + map (1963); Utech & Iltis in *Trans. Wisconsin Acad. Sci.* **58**: 337, map 5, f.1 (1970); Mohlenbr., *Ill. Fl. Illinois,* Hollies to Loasas: 29, t. 10 (1978); Scoggan, *Fl. Canada* **3**: 1097 (1978); Swink & Wilhelm, *Pls of Chicago* region, rev. ed.: 390 (1979); Kaul in Great Plains Fl. Ass., *Fl. Great Plains*: 239 (1986). Type: Cult. in Hort. kew., n.d. (fl & fr), [*Aiton*?] (BM!-holotype).

H. amplexicaule Lam., *Encycl.* **4**: 147 (1797), non Gilib. (1782). Type: Cult. Paris (Jardin des plantes) ex N. America (P-LAM-holotype).

H. ascyroides Willd., *Sp. pl.* **3**: 1443 (1802): Pursh, *Fl. Amer. sept.*: 374 (1814); Nuttall, *Gen. N. Am.*: 16 (1818); Bigelow, *Fl. Bost.* 2nd ed.: 279 (1824); Hooker, *Fl. bor.-amer.* **1**: 109 (1840). Type: Habitat in Pensylvania, *Muhlenberg* s.n. (B-WILLD-holotype, microfiche!).

H. macrocarpum Michx., *Fl. bor-amer.* **2**: 82 (1803); Sprengel, *Syst. veg.* **3**: 342 (1826). Type: Canada, circa Montreal, *Michaux* s.n. (P-holotype).

H. ocymoides Loddiges, *Cat. Pl. Conrad Loddiges & Sons, Hackney*, 15th ed.: 71 (1830), nomen.

Roscyna americana Spach, *Hist. nat. vég.* Phan. **5**: 431 (1836), in *Ann. Sci. Nat. Bot.* II, **5**: 364 (1836). Type as for *H. pyramidatum* Aiton

H. ascyron sensu Coulter in *Bot. Gaz.* **11**: 83 (1886); Jones & Fuller, *Vasc. Pls Illinois*: 324, map 795 (1955); Gillett & Robson in *Publs Bot., Natl. Mus. Nat. Sci. Canada.* no. 11: 23, t. 9, map 7 (1981); Magee & Ahles, *Fl. Northeast* : 737 (1999) et auct. Amer. plur.

Hypericum ascyron var. *americanum* (Spach) Y. Kimura in Nakai & Honda, *Nova fl. jap.* **10**: 124 (1951).

Icones: Vent., *Jard. Malm.* **2**: t. 118 (1804); Mohlenbr., *Ill. Fl. Illinois*, Hollies to Loasas: 29, t. 10 (1978).

Plant 0.5–2 m tall. *Leaves* 40–80 × 18–33 mm, ovate-lanceolate to lanceolate or oblong, base cordate to rounded. *Flowers* 40–70 mm in diam. *Sepals* 8–13 mm wide, ovate to lanceolate or oblong-elliptic, acute to shortly acuminate. *Styles* 3–7 mm, 0.8–1.5 × ovary, almost free or rarely up to 0.8 united. *Capsule* ovoid.

Canada (Quebec, Ontario, Manitoba?), U.S.A. (north-east, from Minnesota to Massachusetts and south to Missouri, Ohio and Maryland).

CANADA. Quebec: Montreal, July 1866 (fl), *Goldie* s.n. (K); Île au Corbeau, 26 May 1859 (fl), *Bourgeau* s.n. (K); Deux-Montagnes, Saint-Columban, 30 August 1936, *Marie-Victorin* 46649 (CM). **Ontario**: London, 17 September 1883 (fl), 5 September 1885 (fr), *Burgess* 343 (BM); L. Huron, Goderich, 19 August 1901, *Macoun* in Herb. Geol. Surv. Canada 34076 (K); Rice Lake Plain, July 1866 (fl), *Macoun* s.n. (K); Lambton Co., 8 km S. of Watford, 17 July 1951 (fl), *Mulligan* 848 (H).

U.S.A. Connecticut: (Magee & Ahles, 1999). **Illinois**: Beardstown, 1842 (fl), *Geyer* s.n. (K); Dixon, pre 2 April 1866 (fl), *Rolfe* s.n. (BM); Augusta, n.d. (fl), *Mead* s.n. (K). **Indiana**: (Crovello, Keller & Kartesz, 1983). **Iowa**: Decora, 20 July 1884 (fl), *Holway* s.n. (H). **Massachusetts**: Boston, n.d. (fl), *B.D.G.* s.n. (K). **Maine**: (Magee & Ahles, 1999). **Maryland**: (Brown & Brown, 1984). **Michigan**: White Pigeon, n.d. (fl), *Carey* s.n. (K); Flint [address], August 1876 (l. fl), *Clarke* 270 (K); Dickinson Co., 6.4 km N. of Norway, 6 August 1961, *Henry* s.n. (CM). **Minnesota**: Minneapolis, 22 July

1991[?1891] (fl), *Sandberg* 613 (H); Little Falls, n.d. (l. fl), *Vasey* s.n. (K); Duluth, junction of Saively Boulevard and Glen Lake, 1942, *Beer* s.n. (CM*). **Missouri**: Watson, 11 July 1894 (fl), *Bush* 37 (K); Atherton, 27 June 1898 (fl), *Bush* 19 (K). **New Hampshire**: (Magee & Ahles, 1999). **New York**: Buffalo, n.d. (fl), *Clinton* s.n. (BM); near Troy, n.d. (fl), *Torrey* s.n. (G-DC, K); upper Susquehanna, along Cheming R., 12 July 1894 (fl & fr), *Lucy & Elmira* 1171 (H). **Ohio**: Portage Co., Mantua township, 15 July 1922, *Webb* s.n. (CM); Wayne Co., near Woostar, 20 June 1910, *Hopkins* s.n. (CM*). **Pennsylvania**: Philadelphia, December 1886 (fl), *Herb. Corstorphine* s.n. (BM); Bethlehem, banks of Lehigh R., 1 October 1849 (fr), *Anon.* s.n. (K); Lawrence Co., Slippery Rock Creek above Wurtemburg, 25 July 1900 (fl & fr), *Shafer* s.n. (CM); Lackawanna Co., Susquehanna R. at Falling Springs, 14 July 1937, *Glowenke* 611 (CM). **Vermont**: (Magee & Ahles, 1999). **Wisconsin**: Palk Co., August 1900 (fl), *Baker* s.n. (JE); Wyoming, n.d. (fl), *Vuran* s.n. (H).

The characteristic features of the American plants, namely acute to acuminate sepals and shortly connate styles, are certainly not constant enough to allow recognition as a species. However, these characters rarely occur together in Asia, where almost free styles are not uncommon but acute sepals appear to be confined to Japan and acuminate sepals are apparently absent. It would seem appropriate, therefore, to give the American plants subspecific rank.

W.G. Dore suggested that the sporadic distribution of *H. ascyron* in Canada, which seems to coincide well with the location of earlier native American Indian camp sites, indicates that this plant was probably distributed by aborigines (Gillett & Robson, 1981: 25), though the reason for this association is not clear.

2. **Hypericum przewalskii** Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 431 (1882), *Mél. Biol.* **11**: 164 (1882), *Fl. tangut.* **1**: 99, t. 18 ff. 1–12 (1889); Forbes & Hemsley in *J. Linn. Soc.* **23**: 74 (1886); H. Léveillé in *Bull. Soc. Bot. France* **54**: 593 (1908); Anon., *Iconogr. Cormoph. Sinicae* **2**: 880, f. 3489 (1972); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 45, t. 12 ff. 4–6 (1990). Type: China, Gansu, parte altae alpina occidentali, ad fl. Yussun-Chatyma, 1880, *Przewalski* s.n. (LE-holotype).

Fig. 10, Map 5.

H. obtusifolium R. Keller in *Bot. Jb.* **33**: 551 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 591 (1908); non Makino (1903). Type: China, Shaanxi, in monte Huan-tou-san, July 1889 (e. fr), *Giraldi* in *Biondi* 3824 (FI!-lectotype, selected here); in rupestribus montis Kian-san, prope Sce-kiu-tsuen che dista circa 65 km, 4 August 1897 (e. fr.), *Giraldi* in *Biondi* 3825 (FI!-syntype).

H. chinense var. *minutum* R. Keller in *Bot. Jb.* **33**: 548 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 590 (1908). Type: China, Shaanxi, Thae-pei-san, 15–20 July 1897 (fl), *Giraldi* in *Biondi* 3837 (FI!-holotype; K!-isotype).

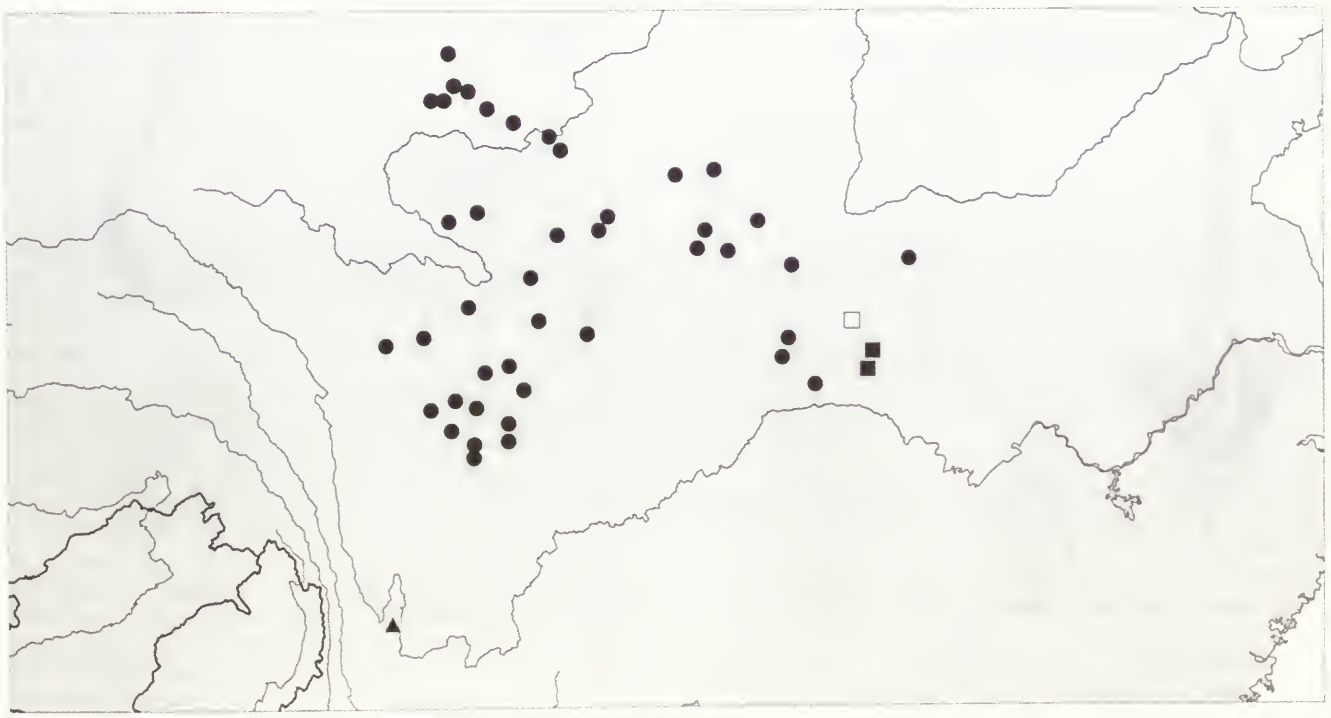
H. pedunculatum R. Keller in *Bot. Jb.* **33**: 549 (1904); H. Léveillé in *Bull. Soc. Bot. France* **33**: 590 (1908); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 71 (1990). Type: China, Shaanxi, Tsil-lin-san, 10 July 1900 (fl), *Giraldi* in *Biondi* 7135 (FI!-holotype).

H. biondii R. Keller in *Bot. Jb.* **33**: 551 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 591 (1908) pro parte quoad spec. cit. *Biondi* 529. Type: China, Shaanxi, in monte Thae-pei-san, August 1899 (e. fr), *Giraldi* in *Biondi* 529 (FI!-lectotype, selected here). The other syntype (*Biondi* 530) is *H. ascyron*.

H. macrosepalum Rehder in Sargent, *Pl. Wilson.* **3**: 451 (1917); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 43 (1990). Type: China, Sichuan, Ta-p'ao-shan, NE of Tachien-lu [Kangding], 3300 m, 5 July 1908 (fl), *Wilson* 2426 (A!-holotype). N.B. Sargent cites the locality as Tai-pei-shan, but the label of the type specimen has it as above.

Icon: Anon. in *Iconogr. Cormoph. Sinicae* **2**: 880, f. 3489 (1972); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 58, t. 12 ff. 1–3 (1990).

Perennial herb (0.17–)0.3–0.55 m tall, erect or sometimes ascending from creeping and rooting base, with stems few to numerous, simple or usually branched below inflorescence or throughout. *Stems* incompletely 4-lined or 2-lined when young, nearly always soon becoming terete; internodes 25–80 mm, shorter than leaves except upper (slightly longer) or rarely all longer. *Leaves* sessile;



Map 5 Sect. 7: 2. *H. przewalskii*, type ●; '*H. pedunculatum*' ■ specimens, other record □; '*H. macrosepalum*' ▲.

Fig. 10 *H. przewalskii*: A. '*pedunculatum*': (a) habit; (b) sepal; (c) petal; (d) ovary. B. *przewalskii*, type: (e) habit; (f) sepal. C. '*macrosepalum*': (g) habit; (h) sepal; (i) ovary (a, e, g × 2/3; rest × 3). A. *Wilson* 582. B. *G.H. Yang* 58812. C. *Pratt* 541.

lamina 20–65(–80) × 10–32 mm, broadly oblong or oblong-ovate to narrowly oblong or oblong-lanceolate (reducing in size down stem), rather paler beneath, not glaucous, plane, chartaceous; apex rounded to shallowly retuse, margin entire, base cordate-amplexicaul; venation: 4–6 pairs of main laterals from lower half of midrib, with subsidiary midrib branches and densely reticulate tertiary venation not or scarcely prominent beneath; laminar glands pale, dense, unequal dots or short streaks; intramarginal glands pale, dense, small. *Inflorescence* 1–7-flowered from 1–3 nodes, corymbiform, sometimes with flowering branches from up to 5 nodes below, the whole then narrowly pyramidal to cylindric; pedicels 12–22 mm (–45 mm in fruit); bracts and bracteoles foliose, ovate, persistent. *Flowers* 20–40 mm in diam., stellate; buds narrowly ovoid to cylindric, obtuse to rounded. *Sepals* 8–10 × 2–4 mm, sometimes enlarging up to 15 × 6.5(–8) mm in fruit, free or basally united, ± imbricate, subequal or unequal or rarely foliaceous, erect in bud, spreading to deflexed in fruit, narrowly or broadly oblong or elliptic to lanceolate or ovate-lanceolate or triangular-lanceolate, rounded to obtuse or rarely shortly mucronate, entire but margin undulate; veins (5)7–9, branching distally and reticulating, midrib scarcely differentiated; laminar glands rather sparse, ± punctiform, distal and submarginal, also a few basal, linear; marginal glands dense, small. *Petals* bright yellow, not tinged red in bud, 12–18 × 4–8 mm, 1.5–1.8 × sepals, oblong-oblanceolate, slightly curved, rounded, without apiculus, margin entire; laminar glands pale, linear, sometimes interrupted distally; marginal glands absent. *Stamen fascicles* 5, each with 15–30 stamens, longest 10–24 mm, *c.* 0.85–1 × petals; anther gland amber. *Ovary* 5(6)–locular, 4–9 × 4–6 mm, ovoid; styles 5(6), 4.5–13 mm, 1–1.8 × ovary, 0.5–0.9 united or appressed (when short); stigmas narrowly capitate. *Capsule* 14–21 × (5)7–14 mm, broadly to narrowly ovoid or subcylindric, 1–2.1 × sepals, obtuse, with numerous narrow longitudinal vittae. *Seeds* dark reddish-brown to greyish-brown, 1.3–1.5 mm, cylindric, not curved, shallowly carinate, without terminal expansion; testa densely shallowly linear-reticulate. 2n = ?

Mountain slopes, river bank thickets, meadows and roadsides; 2150–3400(–4000) m.

China (Gansu, Shaanxi, Henan, west Hubei, Sichuan, north Yunnan, Qinghai).

CHINA. Gansu: T'ao R. basin, meadows of Toyuku, near Choni, 2550 m, July 1925 (fl), *Rock* 12909 (E, K, PE); Wushan Xian, Laojunshan, 1600 m, 30 May 1956 (fr), *Huanghe Exped.* 4241 (PE). **Shaanxi**: Monte Hua-tzo-pin, 20 June 1894 (fl), *Giraldi* in *Biondi* 533 (FI); Tai-pei-shan, 1910 (fl), *Purdom* s.n. (K); Zhashui Xian, Laolin Gongshe, 2200 m, 14 June 1973 (fl), *Hou X.X.* 1888 (IBSC). **Henan**: Luanchuan Xian, 1959 (fr), *Anon.* in *Herb. Beijing Inst. Bot.* 20661 (IBSC). **Hubei**: Fang Hsien uplands, August 1907 (fl), *Wilson* 582 (BM, E, K, NY); Badong Xian, Shennongjia, Niudongwan, 2100 m, 23 July 1957 (fl), *Fu G.X. & Zhang Z.S.* 1033 (IBSC, NAS). **Sichuan**: Kangding Xian (Tatsien-lu), 2700–2870 mm, 25 September 1928 (fr), *Fang* 3545 (E, GH, K, US); Zhegu Shan, 3300 m, 19 August 1957 (fr), *Zhang Z.Y. & Zhou H.F.* 23864 (IBSC); Li Xian, Dabanzhao, 3650 m, 28 June 1957 (fr), *He D.P.* 44559 (SZ). **Yunnan**: Lichiang Range, 1933 (fr), *McLaren's Collectors* s.n. (BM). **Qinghai**: Yellow R. banks, SE of Radja, 3300 m, June 1926 (fl), *Rock* 14213 (E, GH, K, NY); Minhe Xian, Niuxinshan Xian, Tangeryuan Xiang, 2740 m, 9 August 1958 (fr), *Zhu Z.Y.* et al. 260 (KUN); Huangyuan Xian, Guayin Forest Distr., 11 July 1958 (fl), *Tsoong P.C.* 8890 (PE).

H. przewalskii is closely related to *H. ascyron*, differing from it essentially by the obtuse to retuse leaf apex and usually 2-lined mature stem internodes. The remarks about variation in style length in *H. ascyron* (p. 53) would seem to apply also to *H. przewalskii*. Where they are short, they seem to be almost free and appressed rather than united.

Two variants of *H. przewalskii* have been given specific rank, but neither would appear to merit it. '*H. pedunculatum*' (Fig. 10A) has longer narrower leaves and is more branched than typical *H. przewalskii* and, on the basis of the Wilson and Giraldi specimens, appeared at first to be distinct. A study of more abundant material from Chinese herbaria, however, revealed a complete intergradation between the two extremes. '*H. pedunculatum*' is the south-eastern-most population of *H. przewalskii*, in western Hubei and adjacent Shaanxi, and the one nearest morphologically to *H. ascyron*.

'*H. macrosepalum*' (Fig. 10C) seems to be aberrant in having more persistently 4-angled internodes, but is otherwise typical of forms of *H. przewalskii* with a one-flowered inflorescence and foliar sepals in fruit from Sichuan and Shaanxi.

[For Sect. 9. *Hypericum* see Part 4 (2, 3).]

Sect. 9a. **CONCINNA** N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **8**: 173 (1981).

Hypericum sect. *Androsaemum* subsect. *Pseudoandrosaemum* R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* **3**(6): 221 (1893); op. cit., 2nd ed., **21**: 177 (1925) pro parte, quoad *H. concinnum* Benth.

Hypericum sect. 9. *Hypericum* sensu N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 320 (1977) pro parte, quoad *H. concinnum*.

Perennial herbs or sometimes *suffrutices* up to 0.45 m tall, with stems erect or sometimes ascending from woody taproot or caudex, glabrous, with dark glands; branching lateral, from lower nodes. *Stems* 4-lined when young, becoming 2-lined to terete, eglandular. *Leaves* opposite, decussate, sessile to shortly petiolate, free, tardily deciduous, often conduplicate, sometimes falcate; lamina entire with venation pinnate, closed, with tertiary reticulation obscure; laminar glands pale and sometimes black, punctiform, equal; marginal gland dots dark, dense, small; ventral resin glands absent. *Inflorescence* 1–*c.* 17-flowered with branching mostly or wholly monochasial, terminal, sometimes with subsidiary branches from 1–2 nodes below; bracts and bracteoles reduced, persistent. *Flowers* stellate, homostylous. *Sepals* 5, free, persistent, erect in fruit, with margin entire to eroded-denticulate; veins 7–11; laminar glands pale, linear; marginal or submarginal glands few, dark or absent. *Petals* 5, persistent, with apiculus absent or almost so; margin entire or undulate-crenate; marginal glands absent or few, dark; laminar glands pale, linear to striiform. *Stamen fascicles* 5, united 2+2+1 (i.e. '3'), persistent, with stamens totalling 40–*c.* 100; central 4 filaments united above the base, the rest at the base; anthers yellow, gland amber; pollen type X. *Ovary* with central column and 3 axile placentae, ∞-ovulate; styles 3, divergent; stigmas narrowly capitate. *Capsule* 3-valved, subcoriaceous?, with valves narrowly longitudinally vittate. *Seeds* cylindric, not carinate or winged or terminally expanded; testa minutely shallowly pitted.

BASIC CHROMOSOME NUMBER (X). 8, ploidy 2.

HABITAT. Dry slopes and ridges; 390–900 m.

DISTRIBUTION. U.S.A. (northern California)

1 species.

1. **Hypericum concinnum** Benth., *Pl. Hartw.*: 300 ('1848', i.e. 1849?); Coulter in *Bot. Gaz.* **11**: 108 (1886), in A. Gray, *Syn. fl. N. Amer.* **1**: 289 (1897); Greene, *Fl. francisc.*: 112 (1891); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* **3**(6): 211 (1893), op. cit. 2nd ed. **21**: 177 (1925); McMinn, *Man. Calif. shrubs*: 351, f. 403 (1939); Abrams, *Ill. fl. Pacific States* **3**: 116, f. 3235 (1951); Jepson, *Man. Fl. Pls Calif.*: 638, f. 631 (1951); Munz & Keck, *Calif. Fl.*: 192, f. 27 (1959), Suppl. (Munz): 18 (1968); Rickett, *Wild Fls of U.S.* **5**: 160, t. 52 (1971?); Kozloff & Beidleman, *Pls San Francisco Bay Region*: 168, t. 32 (1994); N. Robson in

Map 6 Sect. 9a: 1. *H. concinnum* ● specimens, other record ○.

Cullen et al., *Eur. Gdn Fl.* **4**: 58 (1995). Type: U.S.A., California, 'in valle Sacramento', *Hartweg* 1670 (K!-holotype; BM!, G!, GH!, W!).

Fig. 9D, Map 6.

H. bracteatum Kellogg in *Proc. Calif. Acad. nat. Sciences* , 2nd ed. **1**: 67 (1873), non Buch.-Ham. ex D. Don (1825) (nom. illegit.). Type: U.S.A., California, Yuba Co., Marysville (fl), *E. W. Garvitt* s.n. (CAS-holotype).

H. seleri R. Keller in *Bot. Jb.* **58**: 192 (1923). Types: U.S.A., California, Marin Co., 'macchia am Abhang des Mount Tamalpais', *C. & E. Seler* s.n. (B†-indicated lectotype); [Amador Co.?] 'im Tal des San Stanislaus River', *A. Stübel* s.n. (B†-syntype).

Icon: Rickett, *Wild Fls of U.S.* **5**: 160, t. 52 (1971).

Perennial herb or sometimes *suffruticose*, 0.15–0.33(–0.45) m tall, bushy, erect or more rarely ascending from woody caudex, rarely rooting at the base, branching at most nodes, with branches strict. *Stems* 4-lined and ± ancipitous at first, eventually terete, eglandular; internodes 3–10 mm, shorter than leaves. *Leaves* sessile to shortly petiolate (to 0.5 mm), tardily deciduous; lamina 13–32 × 1.5–8 mm, narrowly elliptic or narrowly oblong to linear (l:b = 4–10), concolorous, glaucescent?, often conduplicate and sometimes falcate, subcoriaceous; apex acute to subacute, margin entire, base cuneate; venation: 2–3(4) pairs of main laterals from lower 2/5 of midrib, with tertiary reticulation obscure and slightly prominent or invisible; laminar glands punctiform, small, pale and sometimes a few black; intramarginal glands black, spaced (10–12). *Inflorescence* 1–*c.* 17-flowered, terminal, often with flowering branches from 1–2 nodes below, the whole then cylindric; pedicels 1–3.5 mm; upper leaf pairs ± bracteose; bracteoles lanceolate to linear-elliptic, entire. *Flowers* 20–35(–40) mm in diam., stellate or reflexed; buds ovoid-cylindric to ovoid, acute. *Sepals* unequal, imbricate, 6–9 × 2–3 mm, broadly to narrowly ovate, acute to acuminate, entire or ± eroded-denticulate; veins 9–11, branching; laminar glands pale, linear to striiform, and rarely 1–2 black, punctiform; marginal glands black, few or absent. *Petals* golden yellow, not red-tinged in bud, (10–)12–15 × 4–5 mm, *c.* 1.7–2 × sepals, obovate to oblong-obovate, apiculus absent or almost so, margin entire or undulate-crenate; laminar glands pale, linear to striiform; marginal glands black, ± numerous, sessile or impressed. *Stamens* 40–80(–100?), '3'-fascicled, longest 8–10(–12) mm, *c.* 0.8 × petals; anther gland amber. *Ovary* 3-locular, 3–4 × 1.8–2 mm, narrowly ovoid; styles 3, 6–9(–12) mm, 2–2.7(–3) × ovary, free, divergent; stigma narrowly capitate. *Capsule* 6–9 × 4–4.5 mm, narrowly ovoid, about equalling sepals; valves longitudinally vittate. *Seeds* dark brown, *c.* 1.5 mm long, cylindric, not carinate or appendiculate; testa minutely and shallowly pitted. 2n = 16 (Raven, Kyhos & Hill, 1965).

Dry slopes and ridges, Yellow Pine (*Pinus ponderosa*) forest, chaparral; 390–600(–900) m.

U.S.A. (California – Sierra Nevada from Mariposa Co. north to Shasta Co., Coastal Ranges from Marin Co. to Mendocino Co.).

U.S.A. California: Marin Co., Mt Tamalpais, 600 m, March 1930 (l. fr), *Meebold* 9798 (K); San Mateo Co.?, near San Francisco, 1866 (fl), *Kellogg*

s.n. (BM, G, W); Napa Co., junction of State highways 37 and 128, 30 May 1957 (fl), *Alava* 989 (W); Mendocino Co., Coastal R.[ange], Eel R., 540–600 m, June 1894, *Purpus* 1148 (K); Amador Co., New York Falls, 600 m, May 1891 (fl), *Hansen* 32 (BM, G, JE, K); Butte Co., Paradise, 27 May 1928 (fl), *Heller* 14560 (G); *Yuba Co., Marysville, n.d.? (fl), *Garvitt* s.n. (CAS).

CULTIVATED. U.S.A. California: Rancho Santa Ana Bot. Gdn [seed ex Marin Co., Mt Tamalpais, Matt Davis Trail, 390 m, coll. *Munz*], 22 June 1955 (fl), *Balls* 10608 (BM).

H. concinnum is the only derivative of sect. *Roscyna* that is directly related to *H. ascyron* subsp. *gebleri*. Unlike nearly all the other derivatives (in sects 9, 9b–d), it has relatively large imbricate sepals and an amber connective gland, characters which, along with its long narrow, usually conduplicate leaves and bushy habit, prompted its removal from its original position in sect. *Hypericum* (Robson, 1977) to a separate section (Robson, 1981). Its isolated geographical location gives added support to this systematic decision; together these facts suggest that it or its ancestor might even have become distinct from *H. ascyron* in Siberia, before crossing to North America. In any case, it does not seem to be directly related to the eastern North American *H. ascyron* subsp. *pyramidatum*.

[For Sect. 9b. *Graveolentia*, see Part 4(3).]

Sect. 9c. **SAMPSONIA** N. Robson **sect. nov.**, sectioni 9d. *Elodeoidibus* affinis sed foliis perfoliatis, capsulae valvis glandulis succiniis ovoideis vel plusminusve elongatis instructis, inter alia differt. A sectioni 8. *Bupleuroides* foliis lanceolatis vel oblongis vel oblanceolatis (haud ovatis vel oblongo-ovatis), sepalis oblongis semper integris, stylis e baso decurvatis, capsula vittis glandiformibus, inter alia differt.

Hypericum sect. 9. *Hypericum* sensu N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 320 (1977) pro parte, quoad *H. sampsonii*.

Perennial herbs or rarely *suffrutices* up to 0.8 m tall, with stems erect or basally decumbent from sometimes woody base, glabrous, with dark glands; branching lateral, from upper or most nodes. *Stems* terete, eglandular. *Leaves* opposite, perfoliate, united, persistent; lamina entire with venation pinnate, closed, with tertiary reticulation rather lax; laminar glands pale or very rarely some black, punctiform, unequal; intramarginal gland dots dark; ventral resin glands absent. *Inflorescence* c. 12–40-flowered with branching mostly dichasial, from 2 nodes, with subsidiary branches from up to 6 nodes below; uppermost bract pair and bracteoles reduced, deciduous, other bracts foliar, persistent. *Flowers* substellate with cupuliform base, homostylous. *Sepals* 5, free, persistent, erect in fruit, with margin entire; laminar glands pale and sometimes dark, striiform to punctiform; intramarginal to marginal glands dark. *Petals* 5, persistent, erect after flowering, without apiculus; margin entire or with ± prominent glands[4]; marginal glands dark, immersed or ± prominent; laminar glands pale, shortly striiform to punctiform, and very rarely also dark, punctiform. *Stamen fascicles* 5, united 2+2+1 (i.e. '3'), persistent, with stamens totalling 15–42; filaments basally united; anther gland dark; pollen type X. *Ovary* with 3 completely or incompletely axile placentae, each ∞-ovulate; styles 3, free, outcurving from base; stigmas broadly to narrowly capitate. *Capsule* 3-valved, chartaceous?, with valves bearing punctiform or ± elongate vesiculate amber glands. *Seeds* cylindric, not carinate or appendiculate; testa finely ribbed-scalariform.

BASIC CHROMOSOME NUMBER (X). Unknown.

HABITAT. Thickets, streamsides, grasslands and marginal areas; 110–1700 m.

DISTRIBUTION. Southern Japan, Taiwan, central and south China, north Vietnam, central Myanmar, India (Meghalaya).

2 species.

Key to sect. 9c. *Sampsonia*

1 Common leaf base expanded; stamens *c.* 0.5 × petals; styles *c.* 2mm, *c.* 0.65 × ovary; ovary 3-locular ..... 1. **sampsonii**

Common leaf base narrowed; stamens *c.* 0.9 × petals; styles *c.* 1mm, *c.* 0.35 × ovary; ovary 1-locular ..... 2. **assamicum**

1. **Hypericum sampsonii** Hance in *J. Bot. Lond.* **3**: 378 (1865), op. cit. **8**: 275 (1870) ['*sampsoni*']; Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **12**: 60 (1867); Franchet & Sav., *Enum. Pl. Jap.* **1**: 55 (1874), op. cit. **2**: 298 (1875); Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **27**: 431 (1882), *Mél. Biol.* **11**: 165 (1882); Forbes & Hemsley in *J. Linn. Soc. Lond.* **23**: 74 (1886); Henry, *List Pl. Formos.*: 19 (1896); Matsum. & Hayata, *Enum. pl. formosan*: 43 (1906); H. Léveillé in *Bull. Soc. Bot. France* **53**: 500 (1906), op. cit. **54**: 593 (1908); Gagnepain in Lecomte, *Fl. Indo-Chine*, **1**: 285 (1909); Hayata, *Icon. pl. formosan.* **1**: 80 (1911); Dunn & Tutcher in *Bull. Misc. Inf. Kew*, Addit. ser. **10**: 41 (1912); Matsum., *Index pl. jap.* **2**: 369 (1912); Makino in Iimuna, *Somoku-Dzusetsu* **14**: t. 30 (1912); Makino & Nemoto, *Fl. Jap.*: 545 (1925), op. cit., 2nd ed.: 752 (1931); R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 180 (1925); Sasaki, *List Pl. Formosa*: 295 (1928); Hand.-Mazz., *Symb. Sin.* **7**: 404 (1931); S. Suzuki in Masamune, *Short fl. Formosa*: 141 (1936); Y. Kimura in *Bot. Mag. (Tokyo)* **54**: 86, f. 7 (1940), in Nakai & Honda, *Nov. fl. jap.* **10**: 127, ff. 45–46 (1951); Ohwi, *Fl. Japan*: 780 (1953), Engl. ed.: 631 (1965); Steward, *Man. Vasc. Pls Lower Yangtze Valley China*: 259 (1958); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 5 (1966); Hatusima, *Fl. Ryukyus*: 416 (1971); Anon. In *Iconogr. Cormoph. Sinicorum* **2**: 880, f. 3490 (1972); N. Robson in *Fl. Taiwan* **2**: 643, t. 433 (1976), 2nd ed. **2**: 710, t. 334 (1996); Momiyama in Satake et al.., *Wild fl. Japan* **2**: 115, t. 110 f. 3 (1982); Li Xiwen in *Fl. R. P. Sinicae* **50**(2) 60, t. 8 ff. 4–7 (1990). Type: China, Guangdong, near Lukpo, *c.* '100 mill. Pass.' W. of Canton [Guangzhou], June 1865 (fl & fr), *Sampson* s.n. (BM!-holotype).

Fig. 11A, Map 7.

H. electrocarpum Maxim. in *Bull. Acad. Imp. Sci. Saint-Pétersbourg* **12**: 62 (1867), *Mél. Biol.* **6**: 261 (1867); Hemsley in *J. Bot., Lond.* **5**: 207 (1876); R. Keller in *Bot. Jb.* **33**: 554 (1904), op. cit. **44**: 49 (1909), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 180 (1925). Type: Japan, Kyûshyû, circa Nagasaki, in fruticetis montium, pluribus locis, 1863 (fl & fr), *Maximowicz* s.n. (LE-holotype; BM!, K!).

H. electrocarpum forma *parvifolium* R. Keller in *Bot. Jb.* **44**: 49 (1909) [*parvifolia*]. Type: Japan, Kyûshû, Fukuoka, in insula Oshima [Tai-kiu], July 1900 (fr), *Faurie* 3872 (Z-holotype; BM!).

H. esquirolii H Léveillé in *Repert. Sp. Nov. Regni Veg.* **6**: 330 (1909), *Fl. Kouy-Tchéou*: 198 (1914). Type: China, Guizhou, Kweichow, 6 July 1905, *Esquirol* 513 (E-holotype).

[4]Kimura (1951) uses 'Petals with fringe of hairs' (i.e. glandular hairs) and Momiyama (1982) uses 'Petals with raised fissures' (raised veins?) to separate *H. sampsonii* from the rest of the Japanese sect. *Hypericum*, as well as the fruit character.

Fig. 11 A. *H. sampsonii*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. assamicum*: (e) habit; (f) sepal; (g) petal; (h) capsule (a, e × 2/3; rest × 6). A. *Fan* 39, except (d) *Faurie* 175. B. *Simon* 180.

Map 7 Sect. 9c: 1. *H. sampsonii* ● specimens, other record ○; 2. *H. assamicum* ■.

H. oshimaënse R. Keller in *Bot. Jb.* **58**: 194 (1923). Type as for *H. electrocarpum* forma *parvifolium*.

Icon: Y. Kimura in Nakai & Honda, *Nova fl. Jap.* **10**: 128, f. 45 (1951); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 46, t. 8 ff. 4–7 (1990).

Perennial herb 0.2–0.8 m tall, erect from decumbent rooting base, with stems single or few, branched above or almost throughout, with branches curved-ascending. *Stems* terete, eglandular; internodes 20–85 mm, exceeding leaves or shorter than them. *Leaves* in perfoliate pairs; lamina (20–)25–70(–80) × (7)10–35 mm, broadly or narrowly lanceolate to oblong or oblanceolate, paler beneath, not glaucous, plane, chartaceous; apex obtuse to rounded, margin entire, common base somewhat expanded, rounded; venation: 4–5 pairs of main laterals from lower half to third of midrib, branching and uniting near margin, with tertiary reticulation not prominent, rather lax; laminar glands all pale to mostly black, punctiform, dense; intramarginal glands black, dense. *Inflorescence c.* 20–40-flowered from 2 nodes, corymbiform, with flowering branches from up to 6 nodes below and uppermost pair sometimes overtopping terminal inflorescence, the whole corymbiform to subpyramidal or cylindric; pedicels 2–3 mm; uppermost bract pair and bracteoles linear-lanceolate to linear, deciduous, other bracts foliar, persistent, all entire. *Flowers* 6–10(–15) mm in diam., substellate with cupuliform base; buds ovoid, obtuse. *Sepals* 5, 3–7(–10) × 1–3 mm, free, unequal, erect in bud and fruit, oblong to oblong-spathulate or linear-oblong, rounded, entire; veins 5(3), branching outward distally; laminar glands ± numerous, pale and rarely black, striiform to punctiform; intramarginal glands irregular, black, rarely absent. *Petals* 5, bright yellow, not red-tinged in bud, 4–8(–13) × 1.5–4(–7) mm, elliptic-oblong, rounded, margin entire or subentire; laminar glands pale (very rarely a few black), shortly striiform to punctiform; marginal glands black, sessile to subsessile. *Stamens* 30–42, longest (2–)3–4 mm, *c.* 0.5 × petals; anther gland black. *Ovary* 3-locular, 2.5–3 × 1.5–2 mm, ovoid to narrowly pyramidal; styles 3, *c.* 2 mm, *c.* 0.65 × ovary, free, outcurving; stigmas broadly capitate. *Capsule* 6–9 × 4–5 mm, broadly ovoid to broadly or narrowly ovoid-pyramidal, exceeding sepals; valves with scattered ovoid to ± elongate amber vesicular glands. *Seeds* orange-brown, *c.* 1 mm long, cylindric, not carinate or appendiculate; testa finely ribbed-scalariform. 2n = ?

Thickets, streamsides, grassy places, roadsides and cultivated margins; 110–1700 m.

China (eastern Gansu to Jiangsu southward, including Hong Kong), Taiwan, Japan (Kyûshû, south Honshû), Vietnam (extreme north), Myanmar (Shan States).

CHINA. Shaanxi: Ziyang Xian, 700 m, 10 August 1959 (fr), *Li P.Y.* 6959 (KUN). **Gansu**: Wen Xian, Fanba Gongshe, Heiyingou, 820 m, 19 August 1976 (fr), *Yang J.X.* et al. 3778 (IBSC). **Henan**: Shangchen Xian, Fushan Xiang, Yuzidian, 110 m, 16 April 1959 (st), *Anon.* in Herb. Beijing Inst. Bot. 12 (PE). **Jiangsu**: Bau Hwa Shan [Baohua Shan], 450 m, 7 June 1922 (fl), *Merrill* 11486 (GH, K, NY), ibid., *Steward* 2120 (K); Yixing Xian, Longchi Shan, 25 June 1962 (fr), *Mao S.H.* 106 (NAS). **Anhui**: Chien Shan Hsien, Tien Chu Shan, 200 m, 11 June 1936 (fl), *Fan & Li* 39 (BM); Taiping Xian, Qidu Gongshe, Longguang Dadui, 400 m, 19 June 1959 (fl & fr), *Anhui Exped.* 822 (IBSC). **Zhejiang**: Hangzhou, 30 May 1957 (fl), *Chang S.Y.*850 (PE); Tianmu Shan, 1 September 1984 (fl), *He X.Y.*29123 (IBSC). **Fujian**: Kushan, near Foochow, 500 m, 10 August 1905 (fr), *Chung* 3738 (SING); Dehua Xian, 700 m, 4 July 1959 (fr), *Huang S.M.* 190743 (IBSC). **Jiangxi**: Kiennan Distr., Sai Hang Cheung, near Tung Lei village, 1–29 August 1934 (fr), *Lau* 4102 (BM, GH); Guixi Xian, Lengshui Xiang, 350 m, 21 July 1958 (fr), *Nie & Lai* 3685 (KUN). **Guangdong**: Yang Shan, S. of Linchow, July–September 1932, *Tsui* 429 (K); Fengchuan Xian, Sike Xiang, 31 May 1958 (fl & fr), *Wand S.* 164186 (KUN). **Guangxi**: Ch'uan Distr., Pai-yun-an and vicinity, 3 June 1937 (fl & fr), *Tsang W.T.* 27599 (US); Lingui Xian, Liangfeng, Yanshan, 10 April 1950 (fl), *Tsoong C.H.* 808129 (IBSC). **Hunan**: inter urbe Hsinhwa et Pantjing, inter vicos Dawan et Gwantjiling, 200–400 m, 30–31 May 1918 (fl), *Hand.-Mazz.* 11981 (K); Heng Shan, Fangguang Temple, 450 m, 5 June 1943 (fl), *Chun S.H.* 3510 (IBSC). **Hubei**: Ichang, 1885? (fl & fr), *Henry* 585 (BM, K, US); Zhuxi Xian, 890 m, 13 September 1959 (fr), *Li P.Y.* 11135 (KUN). **Sichuan**: Emei Xian, Emei Shan, 1300 m, 10

July 1941, *Feng W.P.* 17249 (A, IBSC); Leibo Xian, Xining 214 Chang, 1500 m, 13 July 1983 (fr), *Cao & He* 120957 (SZ); Tianqan Xian, 910 m, 10 June 1982 (fl), *Peng D.Y.* 45433 (CDBI). **Guizhou**: au-dessus de Chong kai, 25 July 1911 (fr), *Esquirol* 3030 (BM); Anlong Xian, Shuangjiang Gongshe, 900 m, *Anshun Exped.* 258 (KUN). **Yunnan**: Nou-yon-se, 27 May 1904 (fl & fr), *Cavalérie* 2030 (K); Suijiang Xian, 850 m, 29 May 1973 (fl & fr), *Sun B.S.* et al. 515 (KUN).

TAIWAN. Taipei: in littore Tamsui, 22 May 1903 (fr), *Faurie* 175 (BM,W); Dandan, Kiirun, 17 May 1930 (fl & fr), *Suzuki* 4469 (TAI). **Taoyuan**: Nankan, Toen, 5 May 1929 (fl & fr), *Kudo* 575 (TAI).

JAPAN. Kyûshû: circa Nagasaki, June 1899 (fl), *Faurie* 3084 (BM); Todoroki valley, 10 May 1933 (st), 16 June 1935 (e. fl), *Greatrex* s.n. (K).

VIETNAM. Bac Phan [Tonkin]: prov. de Hoa-binh, à Kim-boi, April 1926 (fl), *Colani* in *Pételot* s.n. (K); Tu-Phap, May 1888 (e. fr), *Balansa* 3774 (K, P*).

MYANMAR. S. Shan States: Möng Noi, Kengtawng, banks of Salween R. below flood level, 210 m, 7 March 1911 (fl), *Robertson* 253 (K).

CULTIVATED. England: Kew, ex China, Jianxi, 14 July 1983 (l. fl), *K. Acc.* 467-82-04934 (K).

Hance (1865) and apparently all succeeding authors placed this species in sect. 13. *Drosocarpium*, on the basis of its gland-dotted capsule valves, despite the large morphological and geographical differences between it and all the species in that mainly south-east European section. Specialisations aside, *H. sampsonii* is morphologically nearest to *H. przewalskii* (sect. *Roscyna*); the perfoliate leaf pairs and glandular-punctate capsule valves would be anomalous in sect. *Hypericum*. It seems appropriate, therefore, to place this species and its very close relative, *H. assamicum*, in a separate section directly derived from *H. przewalskii*.

2. **H. assamicum** S.N. Biswas in *Webbia* **25**: 671 (1971), in Sharma & Sanjappa, *Fl. India* **3**: 52 (1993). Type: India, Meghalaya, Sylhet, Nowgong, March 1848 (fl & fr), *Simons* s.n. (CAL-holotype and isotype). The Kew and/or Bogor specimens cited below are very likely part of the same *Simons* collection.

Fig. 11B, Map 7.

H. sampsonii sensu Dyer in Hook. f., *Fl. Brit. India* **1**: 255 (1875) pro parte excl. typum.

Icon: Biswas in *Webbia* **25**: 672 (1971).

Perennial or sometimes *suffruticose herb* 0.2–0.3(–0.4) m tall, erect, with stems often many from stout woody base. *Stems* terete; internodes 2–6.5 mm, shorter than to exceeding leaves. *Leaves* in perfoliate pairs; lamina 15–50 × 6–15 mm, oblong to oblanceolate, often suddenly somewhat narrowed below middle, glaucous beneath, plane, thinly chartaceous; apex obtuse to rounded, margin entire or rarely 'glandular-crenulate', base broadly cuneate to rounded, common base narrowed; venation: 2–3(4?) pairs of main laterals usually from lower third to half of midrib, branching and uniting near margin, with tertiary reticulation not prominent; laminar glands black, punctiform, dense; intramarginal glands black, dense. *Inflorescence c.* 12–18-flowered from 2 nodes, corymbiform, with flowering branches from up to 2 nodes below, the whole then corymbiform to subpyramidal; pedicels 1–10 mm; uppermost bracts and bracteoles linear-subulate, other bracts foliar. *Flowers c.* 12 mm in diam., apparently stellate; buds ovoid-ellipsoid. *Sepals* 5, 5–8.5 × 1–2 mm, free, unequal, erect in bud and fruit, 3 larger oblanceolate-spathulate, 7–8.5 × 2 mm, 2 smaller oblanceolate to narrowly oblong, 5–5.5 × 1 mm, obtuse to acute, entire or with subapical marginal glands prominent; veins 3, midrib branched; laminar glands rather few, pale and sometimes black, punctiform; intramarginal to marginal glands irregularly spaced, black. *Petals* 5, 'yellowish', not tinged red in bud, *c.* 5 × 1.7 mm, oblanceolate-spathulate, subobtuse or obtuse, margin entire? or with marginal glands ± prominent; laminar glands pale, striiform to punctiform, and a few black, punctiform; intramarginal to marginal glands black, immersed to sessile. *Stamens c.* 15, longest 4–5 mm, equalling petals or almost so; anther gland black. *Ovary* 1-locular with intrusive placentae, *c.* 2.7 × 2 mm, ovoid; styles 3, *c.* 1 mm, *c.* 0.35 × ovary, free, erect; stigmas capitellate. *Capsule* 5–6 × *c.* 4 mm, cylindric-subglobose, about equalling sepals, valves with scattered punctiform amber vesicular glands. *Seeds* reddish brown, *c.* 0.8 mm long, cylindric, not carinate or appendiculate; testa finely ribbed-scalariform.

'Jungles'; lowland.

India (Meghalaya).

INDIA. Meghalaya: Nowgong, 27 March 1885 (fl), *Clarke* 37671 (K); Nowgong, n.d. (fl & fr), *Simons* 180 (K); no loc., n.d. (fr), *Simons* s.n. (BO); Nowgong, March 1848, *Simons* s.n (CAL*); Mopung, July 1855, *Anon.* s.n. (CAL*); Nowgong (Bramaputra plains), *Kurz* s.n. (CAL*).

H. assamicum is clearly closely related to *H. sampsonii*; the question is whether or not it is distinct. With two possible exceptions all its characters are derivative relative to those of *H. sampsonii*, and so it can be seen as a development from the south-eastward distributional 'arm' of *H. sampsonii* through Yunnan to south-eastern Myanmar on the Salween River. This 'outstation' of *H. sampsonii* is *c.* 850 km from the only locality of *H. assamicum*, in the Bramaputra plains of Assam.

H. assamicum can be distinguished from *H. sampsonii* by the narrowed (not expanded) common leaf base, the longer stamens, the unilocular ovary with relatively and absolutely shorter styles and possibly the more clumped habit with woody base. Of these characters, only the narrowed common leaf base and longer stamens are possibly not derivative. Relative to *H. sampsonii,* it is therefore probably a neo-endemic.

Sect. 9d. **ELODEOIDA** N. Robson, **sect. nov.**, sectioni 9. *Hyperico* similis, sed caulis teretibus eglandulosis, bracteis et bracteolis et interdum foliis superioribus glanduloso-marginatis et auriculis glandulosis instructis, differt; a sectioni 9e. *Monanthema* inflorescentia 1–c. 50-floribus, petalis margine integris vel glanduloso-ciliatis post anthesin erectis, foliis glandulis laminaribus maioribus densis, differt.

Hypericum sect. *Hypericum* sensu N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 320 (1977) pro parte quoad *H. seniawinii* et *H. petiolulatum.*

Hypericum sect. *Adenosepalum* sensu N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 335 (1977) pro parte quoad *H. elodeoides* et *H. napaulense.*

Perennial herbs up to 1 m tall, with stems erect to prostrate, creeping and sometimes branching at base, glabrous, with dark (black or rarely red) glands on leaves, sepals (rarely absent), petals and anthers; branching lateral, from various nodes. *Stems* (mature) terete or rarely (when slender) 2-lined, eglandular. *Leaves* opposite, decussate, sessile or up to 10 mm pseudopetiolate, free, persistent; lamina entire or sometimes wholly or proximally gland-fringed, sometimes with gland-fringed auricles, with venation pinnate, closed and tertiary reticulation dense to lax; laminar glands punctiform, pale and/or black, relatively large (cf. sect. 9e), dense; marginal glands dark, dense to sparse; ventral resin glands absent. *Inflorescence* 1–*c.* 50-flowered, with branching dichasial and/or monochasial, from 1–4(–6) nodes, often with subsidiary branches below; bracts and bracteoles entire to gland-fringed and often glandular-auriculate, reduced. *Flowers* stellate or rarely infundibuliform, homostylous. *Sepals* 5, free, persistent, erect or rarely spreading in fruit, with margin entire to glandular-ciliate; veins 3–5; laminar glands pale and/or dark, linear to punctiform; marginal and/or intramarginal

glands dark. *Petals* 5, persistent, erect after flowering, with or without apiculus, margin entire, with or rarely without immersed or sessile dark glands, or glandular-ciliate; laminar glands pale and/or dark, linear to punctiform, or rarely absent. *Stamen fascicles* 5, united 2+2+1 (i.e. '3'), persistent, with stamens totalling 9–*c.* 60; filaments basally united; anther gland dark; pollen type X. *Ovary* with 3(4) completely axile placentae, each ∞-few-ovulate; styles 3(4), free, divergent from discrete bases; stigmas narrowly capitate to claviform. *Capsule* 3(4)-valved, chartaceous to papyraceous, with valves longitudinally vittate. *Seeds* cylindric, not (rarely scarcely) carinate or appendiculate; testa scalariform-reticulate to scalariform or foveolate.

BASIC CHROMOSOME NUMBER (X). 8; ploidy 2, 4.

HABITAT. Forests, forest margins, slopes, grasslands, roadsides, and sometimes damp meadows and ricefields; (118–)500–3600 m.

DISTRIBUTION. East and south-east Asia from China (Shaanxi, Henan and Anhui southward) to north Vietnam, and west along the Himalaya to Kashmir.

5 species (+ 2 subspecies).

Key to sect. 9d. *Elodeoida*

1 Sepals entire or occasionally with few glandular cilia; bracts without or with short glandular auricles; leaves all entire 2

Sepals regularly or rarely irregularly glandular-ciliate; bracts and sometimes at least upper leaves glandular-ciliate and with glandular-ciliate auricles 5

2(1) Petal laminar glands pale; leaves pseudopetiolate or, if sessile, then narrowly oblong to oblong-lanceolate (l:b = 3–4) 3

Petal laminar glands all or mostly black; leaves sessile, triangular-ovate to ovate-oblong (l:b = 2–3.2) ..... 4b. **H. elodeoides** subsp. **wardii**

3(2) Leaves sessile or with broad petiole to 1 mm, base subcordate-amplexicaul to cuneate; sepals with marginal glands in a ± regular row; styles 2.5–10 mm, c. 1.5–3 × ovary ..... 1. **H. seniawinii**

Leaves with petiole 1–10 mm, base usually cuneate to angustate; sepals with few irregularly spaced marginal glands or none; styles 1–2.5 mm, c. 0.7–1.3 × ovary (2. **H. petiolulatum**) 4

4(3) Styles 1.5–2.2 mm, 1–3 × ovary; leaves broadest at or below middle; inflorescence from 2–3 nodes; stems erect to decumbent ..... 2a. **H. petiolulatum** subsp. **yunnanense**

Styles 1–1.5 mm, *c.* 0.7 × ovary; leaves broadest at or above middle; inflorescence usually from apical node only; stems decumbent to prostrate ..... 2b. **H. petiolulatum** subsp. **petiolulatum**

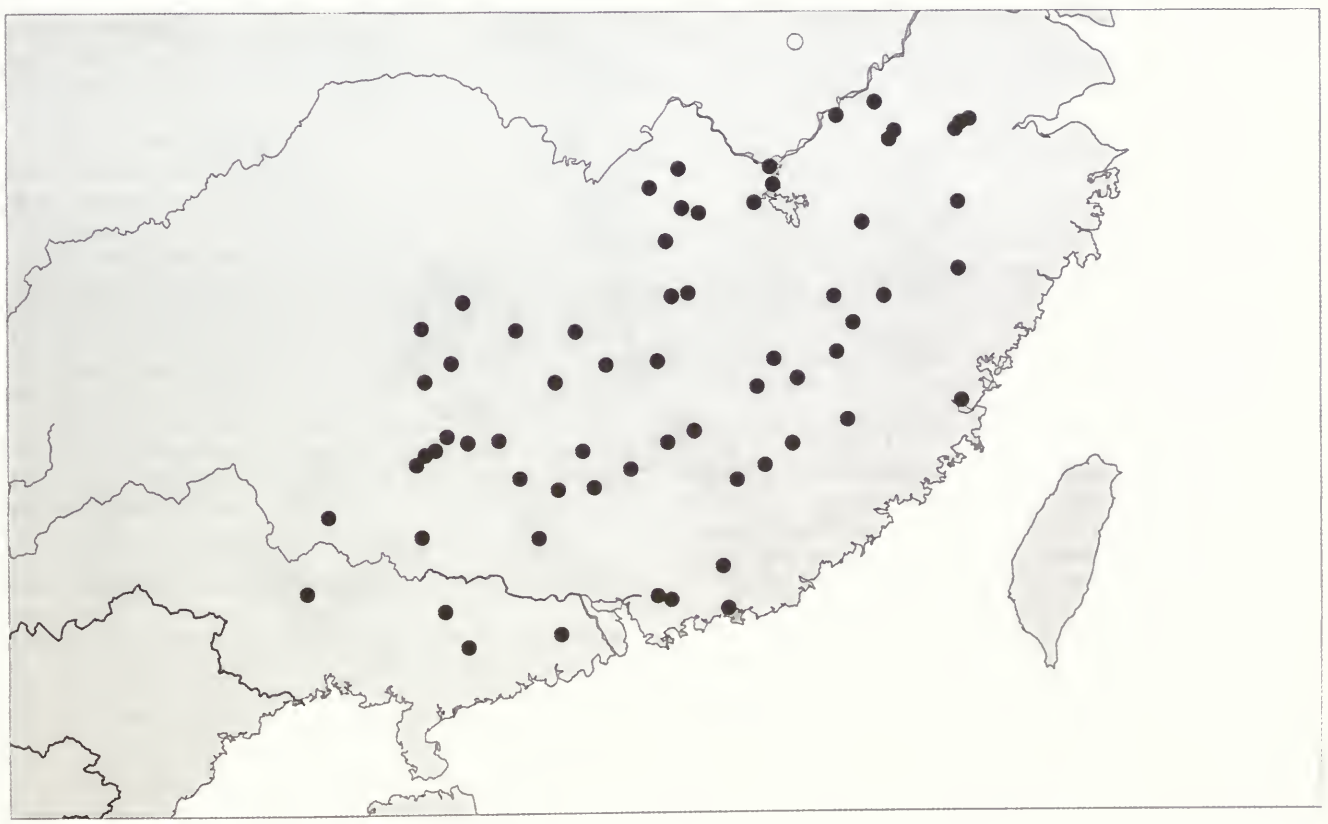
5(1) Leaves lanceolate to oblong-lanceolate or linear, 10–60 mm long, sometimes glandular-ciliate; styles (3–)4–18 mm long, 2–7 × ovary .. 6

Leaves broadly ovate-oblong or broadly elliptic to suborbicular, 6–14 mm long, entire; styles *c.* 3 mm long, 1.5 × ovary ..... 5. **H. kingdonii**

6(5) Styles 3–7 × ovary, 6–18 mm; pedicels 0.5–3(–6) mm; petal laminar glands pale; leaves obtuse to rounded ..... 3. **H. hengshanense**

Styles *c.* 2 × ovary, (3)4–8 mm; pedicels 3–12 mm; petal laminar glands all or mostly black; leaves usually acute ..... 4a. **H. elodeoides** subsp. **elodeoides**

1. **Hypericum seniawinii** Maxim. in *Bull. Acad. Sci. Imp. Saint-Pétersbourg* **27**: 434 (1882), *Mél. Biol.* **11**: 169 (1882); H. Léveillé in *Bull. Soc. Bot. France* **54**: 595 (1908); Hand.-Mazz.,



Map 8 Sect. 9d: 1. *H. seniawinii* ● specimens, other record ○.

Fig. 12 A. *H. seniawinii*: (a) habit; (b) sepal; (c) petal; (d) ovary; (e) capsule; (f) habit (narrow-leaved form). B. *H. petiolulatum* subsp. *yunnanense*: (g) habit; (h) sepal; (i) petal: (j) ovary; (k) capsule. C. *H. petiolulatum* subsp. *petiolulatum*: (l) habit; (m) petal; (n) ovary; (o) capsule (a, f, g × 2/3; rest × 6). A. *H.H. Chung* 2879, except (f) *Ford* 16. B. *Maire* 292, except (g) *Maire* 698. C. *Kingdon Ward* 13270, except (l) *Stainton, Sykes & Williams* 3374.

Symb. Sin. **7**: 402 (1931); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 5 (1966); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 66, t. 13 ff. 1–6 (1990). Type: China, E. China australior, n.d. (fl), *Seniawin* s.n. in Herb. Fischer (LE-holotype). Handel-Mazzetti (1931) noted that the type could not be found in Leningrad.

Fig. 12A, Map 8.

H. lateriflorum H. Léveillé in *Bull. Soc. Agric. Sarthe* **39**: 322 (1904), in *Bull. Soc. Bot. France* **54**: 595 (1908), in *Repert. Spec. Nov. Regni Veg.* **6**: 375 (1909), *Fl. Kouy-Tchéou*: 198 (1914). Type: China, Guizhou, environs de Kouy-yang [Guiyang], a Tchang-chao-sé, 29 August 1899, *Bodinier* 2708 (E-holotype).

H. elodeoides sensu Hand.-Mazz., *Symb. Sin.* **7**: 403 (1931) pro parte quoad spec. cit. (*Wang* 447).

Icon: Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 63, t. 13 ff. 1–6 (1990).

Perennial herb (0.15–)0.3–0.6 m tall, erect from creeping, rooting and sometimes branching base, with stems usually single, sometimes branched above, with branches virgate to curved-ascending. *Stems* terete, eglandular; internodes 20–55 mm, shorter than leaves or usually exceeding them. *Leaves* sessile or with broad 'petiole' to 1 mm; lamina (15–)20–50 × 5–13 mm, oblong to oblong-lanceolate, paler and rarely minutely papillose (Guangdong) beneath, not glaucous, plane, chartaceous; apex obtuse to rounded, margin entire, base subcordate-amplexicaul to broadly or narrowly cuneate; venation: 3(4) pairs of main laterals from lower third of midrib, with tertiary reticulation not prominent, dense; laminar glands pale, dense, rather large; intramarginal glands all black or the occasional one pale, dense. *Inflorescence c.* 5–50-flowered, from 1–3 nodes, densely subcorymbose to broadly pyramidal, with flowering branches from up to 9 nodes below (often with a 'gap' of sterile nodes), the whole then cylindric; pedicels 1–2 mm; bracts and bracteoles ovate to linear-lanceolate, entire or occasionally with basal glandular cilia or rudimentary auricles, persistent. *Flowers* 9–15(–*c.* 20) mm in diam., infundibulariform to stellate or recurved; buds ellipsoid, acute to obtuse. *Sepals* 5, 2.5–5 × 1–2 mm, subequal to equal, erect in bud and fruit, oblong-lanceolate, acute, entire or subentire; veins 5(3), unbranched or outer pairs partly united; laminar glands pale, linear to striiform; marginal glands all black or rarely a few pale, in regular or interrupted row, sessile or slightly prominent. *Petals* 5, bright? yellow, not tinged red in bud, 7–10 × 2–3 mm, 2–3 × sepals, narrowly oblong to narrowly oblanceolate-elliptic, margin subentire, laminar glands pale, striiform to punctiform or absent; marginal glands black, distal, sessile or more proximal immersed. *Stamens* 24–*c.* 50, '3'-fascicled, longest 5–12 mm, slightly shorter than petals; anther gland black. *Ovary* 3-locular, *c.* 1.5–3 × 0.7–1.3 mm, narrowly ovoid; styles 3, (2.5–)4–10 mm, *c.* 1.6–3 × ovary, free, divaricate-incurved; stigmas narrowly capitate. *Capsule c.* 5–6 × 4–5 mm, ovoid, exceeding sepals; valves with dense longitudinal vittae. *Seeds* yellowish brown, *c.* 0.5 mm long, scarcely carinate; testa finely foveolate. 2n = ?

Slopes, grasslands and roadsides; (118–)500–1600(–2000) m.

South-east China (Henan, Anhui and Zhejiang south to Guangxi and Guangdong).

CHINA. Henan: Kikungshan, 9 August 1925 (fl), *Steward* 2728 (K). **Anhui**: Chiu Hwa [Jiuhua] Shan, 500 m, 30 July 1934 (fl & fr), *Fan & Li* 14 (NAS); Huang Shan, 4 August 1935 (fl), *Liou & Tsoong* 10992 (PE). **Zhejiang**: Tien-mu-shan, 2 October 1947 (fr), *Y.W. Law* 1183 (K, PE); Longquan Xian, 1100 m, 26 July 1930 (fl), *Shan R..H.* 5415 (KUN). **Fujian**: Yenping, Cha-ping, 730 m, 2 August 1924 (fr), *H.H. Chung* in Herb. Univ. Amoy 2879 (BM, K); Shanghang Xian, 1400 m, 20 October 1932 (fr), *Ling Y.* 4063 (PE); **Jiangxi**: Lu Shan, Xianrendong, 118 m, 12 July 1955 (fl), *Li B.G.* 085 (IBSC); Yongxiu Xian, near Sa-tiu-hong, 800 m, 21 August 1932 (fl), *Tsiang Y.* 10623 (IBSC, NY); Hong San, 920 m, June–July 1936 (fl), *Gressitt* 1651 (BM); prope oppidum Ningdu ad margines agrorum montis Wuhwa-schan, *c.* 800 m, 21–23 July 1921 (fl), *Wang T.H.* 447. **Guangdong**: Loh-Fan Shan, near Siu Liu waterfall, *c.* 1050 m, August 1920 (fl), *Whiting* s.n. (K); Renhua Xian, Changjiang Xiang, 1670 m, 26 August 1958 (fl), *Tang L.* 7211 (KUN). **Guangxi**: Rong Xian, Tiantangshan, Laoyachong to Tiesuoling, 880–1160 m, 30 June 1956 (fl), *Chun S.H.*9713 (IBSC, KUN); Longshen Xian, Dadi Xiang, 2 July 1955 (fl), *Guangfulingu Exped.* 00614 (IBSC). **Hunan**: in monte Yün-schan prope urbem Wukang, 1200 m, 9 July 1918 (fl), *Handel-Mazzetti* 2543 (K); Chengbu Xian, Dongtouwan, 1 July 1959 (fl), *Tam P.C.* 63643 (IBSC). **Hubei**: Tongshan Xian, 650 m, 11 November 1974 (fr), *Dai L.Y.* et al. 2520 (WH); no precise locality, 1885–1888 (fl), *Henry* 7352 (GH). **Sichuan**: [Nanchuan Xian, 1200 m, 6 July 1957 (fl), *Tsiung & Zhou* 91838 (PE). This is probably an error for *H. petiolulatum* subsp. *yunnanense*]. **Guizhou**: environs de Kouy-Yang [Giuyang], a Tchong-tchao-se, 29 August 1899, *Bodinier* 2708 (E*).

H. seniawinii and the very closely related *H. hengshanense* appear to be south-eastern derivatives of the *H. pedunculatum* form of *H. przewalskii*. *H. seniawinii* differs from *H. hengshanense* in lacking glandular auricles on the leaves but sometimes it bears them on the bracts and bracteoles. The leaves are usually relatively narrow compared to those of *H. hengshanense* but in both species the leaves become markedly narrower towards the south of their respective ranges. *Wang* 447 (Jiangxi) is intermediate in having glandular-ciliate bracts and sepals and glandular-auriculate bracts, but the leaves all lack glandular auricles and all except the uppermost are shortly and broadly petiolate. For differences between it and *H. petiolulatum*, see the latter (p. 70).

2. **Hypericum petiolulatum** Hook. f. & Thomson ex Dyer in Hook. f., *Fl. Brit. India* **1**: 255 (1874); H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908) pro parte quoad typum; N. Robson in *Blumea* **20**: 261 (1972) excl. locc. Sumatra et Sabah, in Hara & Williams, *Enum. Fl. Pls Nepal* **2**: 62 (1979); Robson & Long in Grierson & Long, *Fl. Bhutan* **1**(2): 378 (1984); Li Xiwen in *Fl. Xizangica* **3**: 279, t. 115 ff. 5–9 (1986), in *Fl. R. P. Sinicae* **50**(2): 64, t. 14 f. 1–4 (1990); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 75 (1993), in *Fl. West Bengal* **1**: 265 (1997); Mukherjee & Chaudhri in *J. Econ. Taxon. Bot.* **20**: 125 (1996). Type: India, Sikkim, 2700 m, 1 August 1849 (fl), *Hooker* s.n. (K!-holotype).

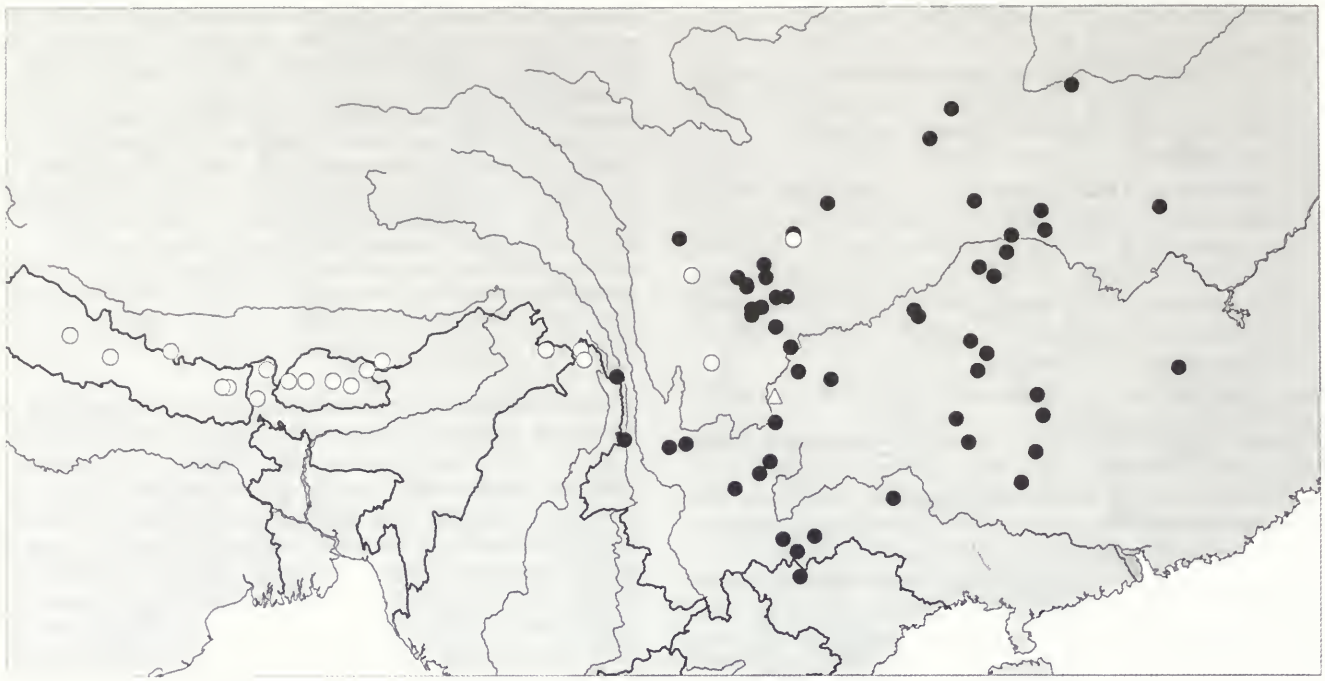
Fig.12B & C, Map 9.

H. thomsonii R. Keller in *Bot. Jb.* **33**: 552 (1904). Type as for *H. petiolulatum* Hook. f. & Thomson non *H. petiolatum* Walter. Note that the specimens cited by Keller belong to *H. subcordatum* (R. Keller) N. Robson; see comments by Handel-Mazzetti (1931: 402).

H. petiolatum sensu R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed., **21**: 179 (1925), orth. mut. vice *H. petiolulatum.*

Icones: see under subspecies.

Perennial (or sometimes *annual*?) *herb* 0.1–0.5 m tall, erect or ascending to procumbent or prostrate from creeping and rooting base, with stems much branched, the branches curved-ascending to spreading or straggling, all or mostly flowering. *Stems* terete, slender, eglandular; internodes much longer than leaves. *Leaves* with petiole 1–7(–10) mm; lamina 5–35(–52) × 3–10(–17) mm, oblong or lanceolate-elliptic to obovate or suborbicular, paler or ± glaucous beneath, chartaceous to submembranous; apex rounded to rarely obtuse, margin entire, base cuneate to angustate or more rarely rounded to subcordate; venation: 3 pairs of main laterals from lower third of midrib, with tertiary reticulation fine, rather dense, not prominent; laminar glands pale, rather large, fairly dense, usually ± prominent, rarely also 1–2 black; marginal glands black, ± dense especially distally. *Inflorescence* (1–)5–28-flowered, from 1–2 nodes, usually with long (1)3–7-flowered branches from up to 5 nodes



Map 9 Sect. 9d: 2a. *H. petiolulatum* subsp. *yunnanense* ●; 2b. *H. petiolulatum* subsp. *petiolulatum* ○ specimens, other record Δ.

below, the whole narrowly to broadly pyramidal; pedicels 4–13 mm; bracts and bracteoles linear (or lower bracts foliar), entire or more rarely with scattered black marginal glands, sessile or on short cilia, and sometimes glandular auricles. *Flowers* 5–8 mm in diam., stellate; buds ellipsoid, obtuse. *Sepals* 5, 2.3–3.2(–3.4) × 0.5–0.9 mm, equal to unequal, erect in bud, ± spreading in fruit, very narrowly oblong-lanceolate or rarely narrowly elliptic-oblong to linear, acute or rarely subacute, entire or occasionally sparsely glandular-ciliate (especially towards base); veins 3, unbranched; laminar glands pale or rarely black, linear to punctiform, variable in size and number; marginal or submarginal glands black or reddish, few (sometimes only apical) or absent. *Petals* 5, bright? yellow, not red-tinged in bud, 3–5.5 × 1–1.2 mm, *c.* 1.5 × sepals, narrowly oblong, acute, margin entire, laminar glands pale, 1–2, punctiform, or absent; marginal glands black, 1–2 near apex and occasionally elsewhere, sessile or immersed. *Stamens* (9–)17–22, '3'-fascicled, longest (2.5–)3–4.5 mm; anther gland black. *Ovary* 3(4)-locular, 1.2–2 × (1–)1.5–2 mm, ± broadly to narrowly ellipsoid; styles 3(4), (0.5–)1–2.5 mm, free, outcurving; stigmas claviform. *Capsule* 3.5–4 × 3.5 mm, broadly ovoid to orbicular, exceeding sepals; valves longitudinally vittate. *Seeds* yellow-brown, 0.5–0.6 mm, not carinate; testa densely but shallowly scalariform-reticulate. 2n = ?

Mountain slopes, thickets and grasslands, stream banks, cliffs, roadsides, forest margins; (250–)1200–3100 m.

China (west and south-west), Vietnam (north), Myanmar (north), India (Arunachal Pradesh, Benghal, Sikkim), Bhutan, Nepal (for records from the Philippines and Sabah see *H. taihezanense*, Part 4(3)).

H. petiolulatum is closely related to *H. seniawinii*, of which it appears to be an upland derivative. It has two subspecies: subsp. *yunnanense* is confined to China and adjacent north Vietnam, whereas subsp. *petiolulatum* is distributed from Yunnan, Sichuan and Xizang along the Himalayan range to Nepal.

H. petiolulatum subsp. *yunnanense* has been confused with smaller-flowered forms of *H. seniawinii* with narrow and/or cuneate-based leaves, but can be distinguished from them by the shorter styles and smaller, broader capsule and usually by the absence or paucity of marginal sepal glands (not in a continuous row). The gap in distribution between these taxa is small, but the above-mentioned differential characters do appear to hold.

2a. **Hypericum petiolulatum** subsp. **yunnanense** (Franchet) N. Robson in *Blumea* **20**: 262 (1973); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 66 (1990). Type as for *H. yunnanense* Franchet.

Fig. 12B, Map 9.

H. yunnanense Franchet in *Bull. Soc. Bot. France* **33**: 437 (1886), *Pl. delavay.*: 103 (1889); H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908). Types: China, Yunnan, in pratis humidis ad Song-pin, supra Tapin-tze, 18 August 1884 (fl & fr), *Delavay* 1943 (P!-lectotype, Robson 1973). The other two collections cited by Franchet belong to *H. monanthemum*.

H. mairei H. Léveillé in *Repert. Spec. Nov. Regni Veg.* **11**: 298 (1912); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 4 (1966); non H. Léveillé (1915). Type: China, Yunnan, Tong-Chuan, 2600 m, June 1910, *Maire* in Herb. Bonati 7492 (E!-holotype).

H. pseudopetiolatum var. *grandiflorum* Pampanini in *Nuovo Giorn. Bot. Ital.* N.S. **17**: 672 (1910). Type: China, Hubei, Jen-kai-kou, 1500 m, 10 July 1905 (fl), *Silvestri* 1492 (FI-holotype, BM!-photo).

H. centiflorum H. Léveillé in *Bull. Géogr. Bot.* **25**: 23 (1915). Type: China, Yunnan, plaine de Tong-Tchouan, 2500 m, August 1912 (l. fl & fr), *Maire* s.n. (E-lectotype, Robson 1973; BM!); plaine et vallons à Tcha-Ho, 2600 m, July 1912 (fl & fr), *Maire* s.n. (E-syntype; BM!).

Icones: none. For figures labelled as subsp. *yunnanense* by Li Xiwen (1973, 1990 – above) see subsp. *petiolulatum*.

Stems erect to decumbent, rooting at base, branches curved-ascending. *Leaf lamina* 15–40 × 6–16 mm, lanceolate or oblong to oblong-lanceolate (broadest at or below middle). *Inflorescence* from 2–3 nodes. *Ovary* 1.5–2.2 mm long; styles 1.5–2.2 mm, 1–1.3 × ovary.

Grassy slopes, roadsides, cliffs, forest margins and grasslands; (350–) 820–3100 m.

South China (Shaanxi and Henan south to Yunnan and Guangxi), north Vietnam.

CHINA. Shaanxi: Zhouzhi Xian, Chenhe Xiang, 1570 m, 10 August 1958 (fr), *Zhang X.M.* 298 (IBSC); Yang Xian, 1700 m, 24 July 1952 (fl & fr), *Fu K.T.* 5182 (PE). **Henan**: Jigong Shan, 9 August 1925 (fl & fr), *Steward* 9835 (US). **Fujian**: Changting Xian, Sidu Gongshe, Louzi Ba, 500 m, September 1993, *Meihuashan Exped.* 35 (IBSC). **Jiangxi**: Fenyi Xian, Dagangshan, 350 m, 28 August 1985 (fl), *Yao K.* 9260 (A, CAS, NY). **Guangxi**: Huaping Forestry Area, 870 m, 14 August 1962 (fl), *Yuan S.F.* 5656 (IBSC); Lingyun Xian, 28 July 1937 (fl), *Lau S.K.* 28791 (A). **Hunan**: Sinning Hsien, Ma-Ling Tung, 600 m, 15 September 1935 (fl & fr), *Fan & Li* 492 (A, BM, W); Dongkou Xian, outskirts of Dongkou Zheng, 330 m, 1910 (fl & fr), *Maire* 1425 (NY); Yunshan to Yangjiapai, 4 September 1950 (fr), *Chang H.T.* 4448 (IBSC). **Hubei**: Badong Xian, Shennongjia, 2300 m, 23 July 1957 (fl), *Fu & Zhang* 1020 (PE); Shenlungkai, 1850 m, 1976 (fl & fr), *Chow K.S.* 76034 (A, BM, K, NY). **Sichuan**: Dujangyan Mun. (Guan Xian), Niangziling Mtn, upstream from Longxi on Longxi R., 1400 m, 4 September 1988 (fl), *Boufford & Bartholomew* 24593 (A*, BM, CAS*, PE*); Nan cuang hien, 1450 m, 15 September 1957(fr), *Xung & Li* 93496 (SZ); Emei Shan, 1700 m, 26 September 1935 (fl & fr), *Tu T.H.* 509 (IBSC, PE). **Guizhou**: Songtao Xian, vicinity of Lengjiaba near confluence of rivers Xiaohe and Duhe, NE side of Fanjing Shan, 820–1120 m, 10 October 1986 (fr), *Sino-American Guizhou Bot. Exped.* 2361 (A); near Leigongshan Muchang, 24 August 1959 (fl & fr), *S. Guizhou (Qiannan) Exped.* 3535 (KUN). **Yunnan**: N. of Mengtze, 2400 m, n.d.(fl), *Henry* 10274 (K); Dali, Cangshan, 7 August 1922 (fl & fr), *Rock* 6413 (A, NY, US); Binchuan Xian, Jizu Shan, 28 September 1940 (fr), *Ching R.C.* 24944 (KUN).

VIETNAM. North: Tonkin, Chapa, c. 1500 m, August 1939 (fr), *Pételot* 2295 (GH).

2b. **Hypericum petiolulatum** subsp. **petiolulatum**
Fig. 12C, Map 9.

H. petiolulatum var. *orbiculatum* Franchet in *Bull. Soc. Bot. France* **33**: 437 (1886), *Pl. delavay.*: 103 (1889); H. Léveillé in *Bull. Soc Bot. Fr.* **54**: 594 (1908). Type: China, Yunnan, ad juga montis Koua-la-po (Hokin) in humidis, 3000 m, 4 August 1885 (fl), *Delavay* 1942 (P!-holotype).

H. humifusum subsp. *orbiculatum* S.N. Biswas in *Bull. Bot. Surv. India* **29**: 53, f. 2 (1989), in Sharma & Sanjappa, *Fl. India* **3**: 67, f. 24 (1993), in *Fl. West Bengal* **1**: 264 (1997). Type: Nepal, near Tagat, 2550 m, 5 July 1954 (fl), *Stainton, Sykes & Williams* 3374 (CAL-holotype; BM!).

Icones: Li Xiwen in *Fl. Xizangica* **3**: 280, t. 115 ff. 5–9 (1986); in *Fl. R. P. Sinicae* **50**(2): 65, t. 14 ff. 1–4 (1990); S.N. Biswas in *Bull. Bot. Surv. India* **29**: 53, f. 2 (1989).

Stems decumbent to prostrate, branches ± diffuse. *Leaf lamina* 5–25 × 4–11(–15) mm, oblanceolate to elliptic or orbicular (broadest at or above middle). *Inflorescence* usually from one node. *Ovary* 1.5–2 mm long; styles 1–1.5 mm, 0.65–0.75 × ovary.

Mountain slope thickets and grassland; 2100–3000 m.

China (Yunnan, Sichuan, Xizang), Myanmar (north), India (Arunachal Pradesh, Benghal, Sikkim), Bhutan, Nepal.

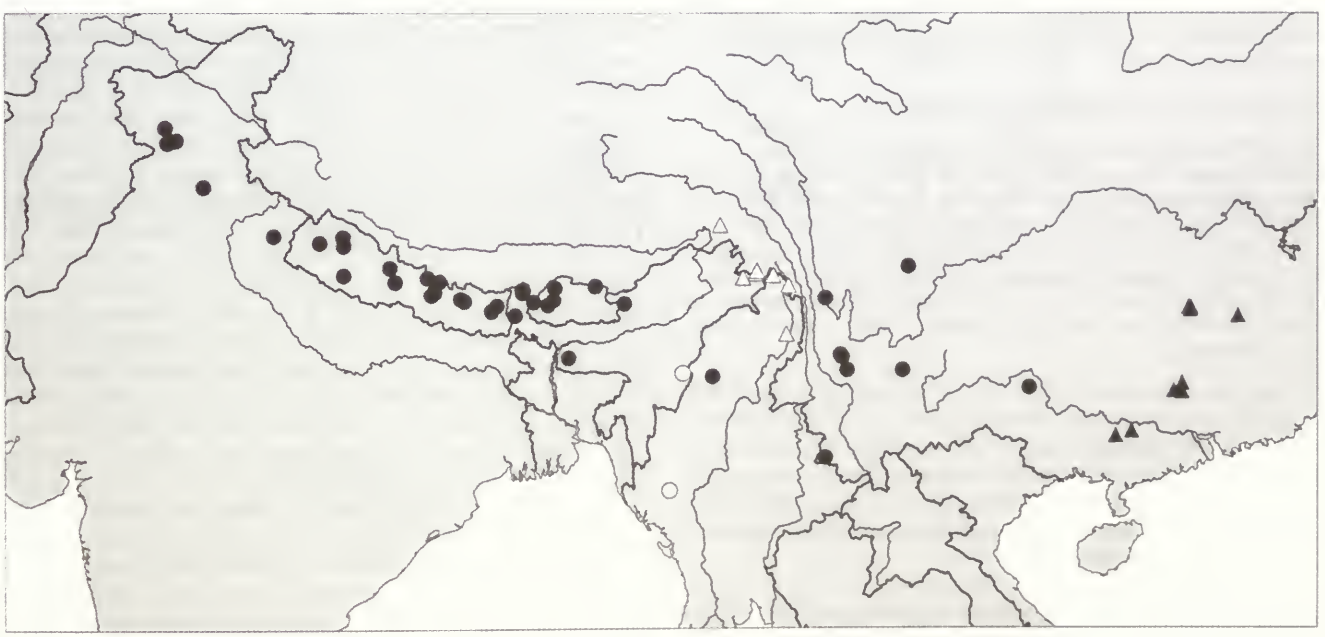
CHINA. Sichuan: Mu li [Muli] hien, 2200 m, 30 August 1978 (fl & fr), *Zhou C.S.* et al. 8212 (SZ). **Sichuan/Yunnan**: Yangpi (Yungpei?) pass, 2490 m, 19 August 1922 (fl & fr), *J.W. & J. Gregory* s.n. (BM). **Yunnan**: Col de Kou-la-po (Hokin), 3000 m, 4 August 1885 (fl), *Delavay* 1962 (P). **Xizang**: Nyalam Xian, 2350 m, 16 August 1972 (fl & fr), *Tibet Medicinal Exped.* 1236 (PE); Cona Xian, 3000 m, 26 August 1975 (fl & fr), *Qingzang Exped.* 75-1594 (KUN, PE).

MYANMAR. Nam Tamai valley, 28° N, 97° 40¢ E, 1200 m, 16 September 1937 (fr), *Kingdon-Ward* 13270 (BM); Nam Tamai valley (Adung Wang), 28° 15¢ N, 97° 35¢ E, 2100 m, 29 September 1937 (fr), *Kingdon-Ward* 13314 (BM).

INDIA. Arunachal Pradesh: Delei valley, 28° 15¢ N, 86° 35¢ E, 3000 m, 23 August 1928 (fr), *Kingdon-Ward* 8575 (K). **Benghal**: Darjeeling, *Mukerjee* et al. 645 (CAL*, DD*). **Sikkim**: Lachen, 2700 m, 1 August 1849 (fl), *Hooker* s.n. (K).

BHUTAN. Tobrang, Trashi Yangsi Chu, 2100 m, 7 July 1949 (fl & fr), *Ludlow, Sherriff & Hicks* 20858 (BM, E*); Chenkaphug, E. of Thimpu, *c.* 3000 m, 20 July 1979 (fl), *Grierson & Long* 2799 (BM, E*).

NEPAL. East: Milka Bhanjzang, 2550 m, 3 July 1969 (fl), *Williams* 1100 (BM). **Central**: above Siklis (S. of Annapurna), 28° 07¢ N, 84° 06¢ E, 29 August 1976, *Troth* 999 (BM, US*). **West**: near Tagat, 2550 m, 5 July 1954 (fl), *Stainton, Sykes & Williams* 3374 (BM, CAL*).



Map 10 Sect. 9d: 3. *H. hengshanense* ▲; Sect. 9d: 4a. *H. elodeoides* subsp. *elodeoides* ●; 4b. *H. elodeoides* subsp. *wardii* ○, Sect. 9d: 5. *H. kingdonii* Δ.

3. **Hypericum hengshanense** W.T. Wang in *Bull. Bot. Lab. N. E. Forest. Inst., Harbin*, no. 5: 27 (1979). Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 59 (1990). Type: China, Hunan, Hengshan, 820 m, 20 July 1948 (fl), *Y. Liu* 109 (PE-holotype, BM!-photo; NAS!). Map 10.

H. hengshanense var. *xinlinense* Z.Y. Li in *Bull. Bot. Res., Harbin* **8**: 129, t. 2 (1988). Type: China, Hunan, Mons Ziyunshan, 1100 m, 13 September 1984 (fl & fr), *Ziyunshan Exped.* 1789 (PE-holotype).

Icones: W.T. Wang in *Bull. Bot. Lab. N.E. Forest Inst., Harbin*, no. 5: 27 (1979); Z.Y. Li in *Bull. Bot. Res. Harbin* **8**: 132, t. 2 (1988).

Perennial herb 0.62–1 m tall, erect from creeping and rooting base, with stems single?, shortly branched above, with branches virgate. *Stems* terete, eglandular; internodes *c.* 30–45 mm, shorter than leaves. *Leaves* sessile; lamina (15–)30–60 × (3–)7–16 mm, oblong-lanceolate to narrowly oblong-elliptic, paler beneath, not glaucous, plane, chartaceous; apex obtuse to rounded, margin entire or ('var. *xinlinense*') black-glandular-ciliate to -denticulate, base slightly oblique-cuneate or (uppermost) rounded, upper pair(s) sometimes with black-glandular-fimbriate auricles; venation: 2(3) pairs of main laterals from lower quarter to third of midrib, with tertiary reticulation dense; laminar glands pale, scattered, large; intramarginal glands black, ± dense. *Inflorescence* 5–*c.* 18-flowered, from (1)2–3 nodes, subcorymbiform to broadly pyramidal; pedicels 0.5–3(–6) mm; bracts and bracteoles linear-lanceolate to linear, with margin and auricles black-glandular-fimbriate. *Flowers* 15–25 mm in diam., stellate; buds ellipsoid, obtuse. *Sepals* 5, 5–8 × 1.5–2 mm, equal, erect in bud and fruit, oblong-lanceolate to linear-oblong, acute, glandular-ciliate; veins 3, unbranched; laminar glands pale, linear to striiform; intramarginal glands few, distal, black, or absent; marginal glands (to 16 on each side) on cilia, black. *Petals* 5, bright? yellow, not tinged red in bud, 9–15 × 2.5–3 mm, *c.* 2 × sepals, narrowly oblong, margin entire?, laminar glands pale, striiform to punctiform, marginal glands black, punctiform. *Stamens* ∞, '3'-fascicled, longest 8–15 mm, 0.6–0.75 × petals; anther gland black. *Ovary* 3-locular, 2-2.5 × *c.* 1–1.5 mm, ovoid; styles 3, 6–18 mm, 3–7 × ovary, divaricate-incurved, 'long-inserted' (Li Xiwen 1990); stigmas narrowly capitate. *Capsule* 5.5–6(–9?) × 3–3.5(–4?) mm, ovoid, exceeding sepals; valves with dense longitudinal vittae. *Seeds* not seen. 2n = ?

Slopes, thickets and roadsides; 600-1100 m.

South China (Jiangxi, Guangdong, northern Guangxi, Hunan).
CHINA. Jiangxi: sine loc., 600 m, 16 July 1964 (fl), *Yang & Yao* 1140 (NAS); Guangchang, Kuang Fang, Yashi Shan, 17 October 1962 (fr), *Yue J.S.* 2523 (IBSC). **Guangdong**: Lianshan Xian, Shangshuai Xiang, 980 m, 11 July 1958 (fl), *Tam P.C.* 58761 (KUN). **Guangxi**: Waitsup Distr., Tong Shan, near Sap-luk Po village, 16 September 1933, *Tsang* 22802 (W); Yuangupo He, Linfan Shan, 30 August 1958 (l. fl), *Li Y.K.* 401127 (IBSC). **Hunan**: Heng Shan, 1–6 June 1943 (st), *Chen Z.D.* 217 (IBSC); see also holotype and that of var. *xinlinense*.

H. hengshanense is closely related to *H. seniawinii*, differing from it by the glandular-auriculate leaves and bracts, the glandular-ciliate sepals and the longer styles. Its very restricted distribution is wholly within that of *H. seniawinii*, and it is morphologically intermediate between that species and *H. elodeoides*. See discussion under 1. *H. seniawinii* (p. 69). The Guangxi populations have smaller, relatively narrow leaves and smaller flowers.

4. **Hypericum elodeoides** Choisy in DC., *Prodr.* **1**: 551 (1824); Dyer in Hook. f., *Fl. Brit. India* **1**: 255 (1874); Franchet in *Bull. Soc. Bot. France* **33**: 438 (1886), *Pl. delavay.*: 104 (1889); H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908) [*helodeoides*]; Burkill in *Rec. Bot. Surv. India* **4**: 99 (1910); R. Keller in Engl. & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 179 (1925); Banerji in *J. Bombay Nat. Hist. Soc.* **51**: 774 (1953), op. cit. **55**: 251 (1958), in *Rec. Bot. Surv. India* **19**(2): 27 (1966); Y. Kimura in Hara, *Fl. E. Himal.*: 209 (1966), op. cit. **2**: 81 (1971); N. Robson in Nasir & Ali, *Fl. W. Pakistan* **32** (Guttiferae): 10 (1973), in *J. Jap. Bot.* **52**: 285, excl. f. 3 (1977), in Hara & Williams, *Enum. Pl. Nepal* **2**: 61 (1979); Robson & Long in Grierson & Long, *Fl. Bhutan* **1**(2): 377 (1984); Li Xiwen in *Fl. Xizangica* **3**: 279, t. 115 ff. 1–4 (1986), in *Fl. R. P. Sinicae* **50**(2): 59, t. 11 ff. 3–7 (1990); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 56, f. 19 (1993), in *Fl. Bengal* **1**: 262 (1997); Mukherjee & Chaudhuri in *J. Econ. Taxon. Bot.* **20**: 125 (1996). Type: Nepal, no precise locality, 1821 (fl), *Wallich* 4812A (G-DC!-holotype; BM!, K!, SING!).
Fig. 13A & B, Map 10.

H. napaulense Choisy in DC., *Prodr.* **1**: 552 (1824). Type: Nepal, no precise locality, 1821 (fl), *Wallich* s.n. (G-DC!-holotype).
H. nervosum D. Don, *Prodr. Fl. Nepal.*: 219 (1825), nom. illegit. superfl. Type as for *H. elodeoides*.
H. pallens D. Don, *Prodr. Fl. Nepal.*: 219 (1825), nom. illegit. superfl., non Banks & Solander (1794). Type as for *H. elodeoides*.
H. adenophorum Wall. [*Numer. List*: 170, no. 4812] ex Dyer in Hook. f., *Fl. Brit. India* **1**: 256 (1874) in synon.

Icones: Li Xiwen in *Fl. Xizangica* **3**: 280, t. 115, ff. 1–4 (1986); in *Fl. R. P. Sinicae* **50**(2): 56, t. 11 ff. 3–7 (1990).

Perennial herb 0.15–0.5(–0.73) m tall, erect (sometimes from creeping and rooting base), with stems caespitose, unbranched or rarely branched above, with branches virgate *Stems* terete, eglandular; internodes 5–35 mm, usually shorter than leaves. *Leaves* sessile; lamina 10–50 × (2–)4–12(–17) mm, lanceolate or more rarely ovate-lanceolate to oblong-lanceolate or oblong-elliptic to linear, paler or glaucous beneath, plane or margins recurved, chartaceous; apex acute to subacute or more rarely obtuse to rounded, margin entire or (upper) glandular-ciliate towards base, base cordate-amplexicaul to rounded, the upper usually with glandular-ciliate auricles; venation: (2)3 pairs of main laterals from lower third to fifth of midrib, usually prominent beneath, with tertiary reticulation lax; laminar glands pale, dense, large, punctiform or shortly striiform; intramarginal glands black, sparse. *Inflorescence* (1–)5–*c.* 30-flowered, from 1(2–4) nodes, corymbiform to cylindric, very rarely with flowering branches from 1–2 nodes below; pedicels 3–12 mm; bracts and bracteoles ovate-lanceolate to oblong-lanceolate or linear, with margin and auricles black-glandular-ciliate or very rarely subentire to entire without auricles. *Flowers* 10–20 mm in diam., stellate; buds ellipsoid. *Sepals* 5, 5–9 × 1–1.5(–3) mm, equal, erect in bud and fruit, narrowly elliptic-lanceolate to narrowly oblong-lanceolate, acute, glandular-ciliate; veins 5, unbranched, prominent; laminar glands pale or black, linear to striiform; marginal glands on cilia and a few sessile, black. *Petals* 5, golden yellow, not tinged red in bud, 7–15 × 3–4 mm, oblanceolate to obovate-oblong, margin entire, laminar glands black and sometimes a few pale, linear to punctiform, dense to sparse, marginal glands black, distal, few, sessile. *Stamens c.* 60, '3'-fascicled, longest 8–11 mm, *c.* 0.75 × petals; anther gland black. *Ovary* 3-locular, 2–4 × 1.3–1.7 mm, narrowly ovoid; styles 3, (3–)4–8 mm, *c.* 2 × ovary, divaricate, curved-ascending or straight; stigmas narrowly capitate. *Capsule* 5–8 × 4–5.5 mm, ovoid, about equalling sepals; valves longitudinally vittate. *Seeds* yellow-brown, 0.5–0.6 mm, not carinate; testa densely scalariform-reticulate. 2n = 16 (n = 8; Sugiura, 1944), 32 (n = 16, Sandhu & Mann, 1989).

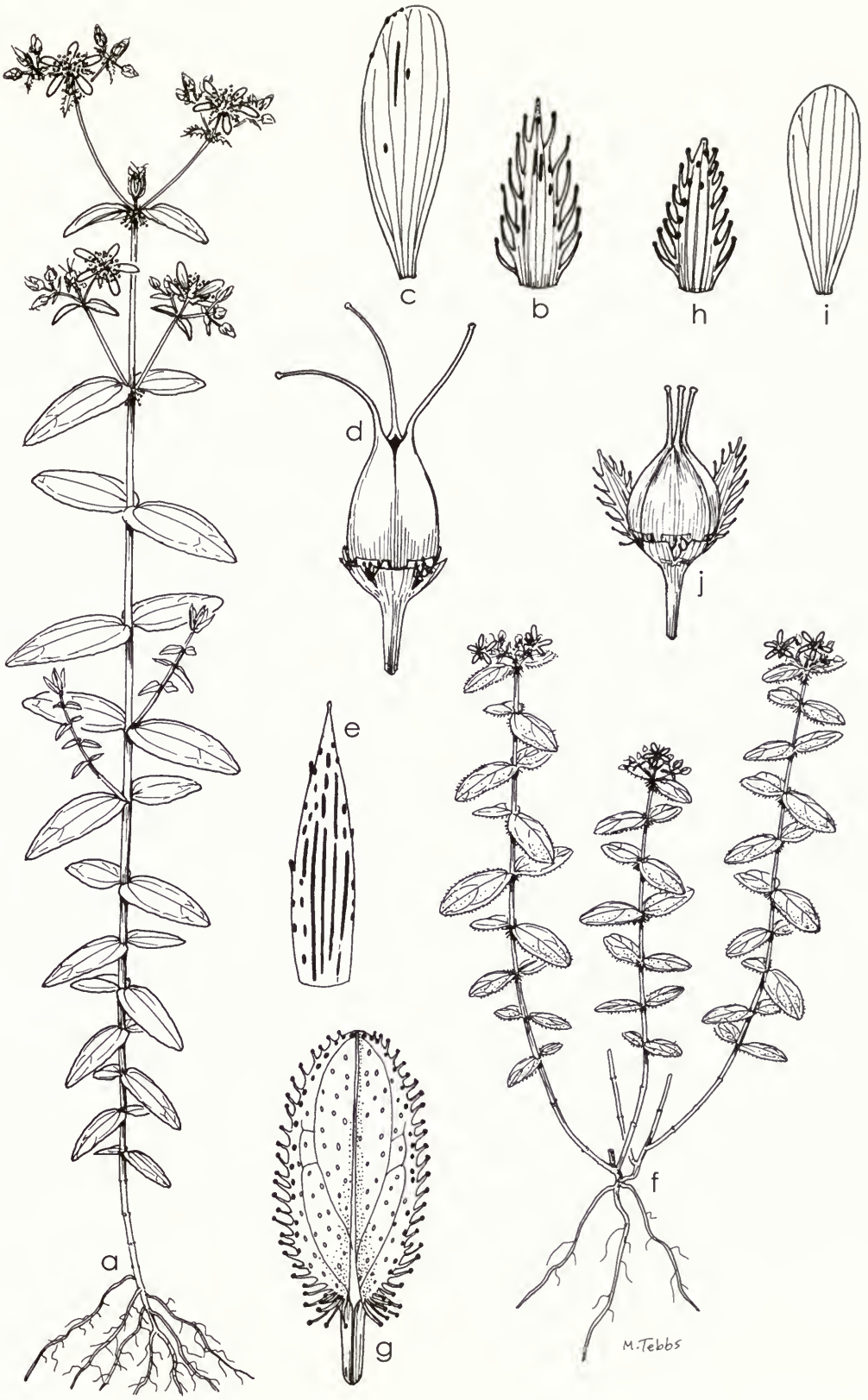


Fig. 13 A. *H. elodeoides* subsp. *elodoides*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. elodeoides* subsp. *wardii*: (e) sepal. C. *H. wightianum*: (f) habit; (g) leaf; (h) sepal; (i) petal; (j) capsule (a, f × 2/3; d, g, j × 4; b, rest × 6). A. *Polunin, Sykes & Williams* 448. B. *Kingdon Ward* 22780. C. *Forrest* 4298.

Forests, forest margins and clearings, thickets, damp meadows and rice fields, grassy slopes and tracksides; (750?–)1050–3600 m.

South China (Guangxi, Sichuan, Yunnan, Xizang; also recorded from Guizhou, Guangdong, Hunan, Hubei, Jiangxi and Fujian), Myanmar (Mt. Victoria), India (Manipur, Meghalaya, Arunachal Pradesh, Benghal, Sikkim, Uttar Pradesh, Himachal Pradesh, Kashmir), Bhutan, Nepal.

H. elodeoides is closely related to *H. hengshanense*, but has shorter leaves and styles and is in general smaller. The main reduction trend in this species, in which the acute leaves gradually become linear, runs mainly east to west along the Himalayan range to Kashmir, omitting north Myanmar and most of Arunachal Pradesh. In a separate, southward trend through Manipur into western Myanmar, however, the leaves remain relatively broad (though smaller) and all become entire and rounded at the apex, and the sepals, bracts and bracteoles also become subentire or entire. These plants have been given subspecific rank as subsp. *wardii*.

4a. **Hypericum elodeoides** subsp. **elodeoides**, Biswas in Sharma & Sanjappa, *Fl. India* **3**: 58 (1993).
Fig. 13A, Map 10.

Leaves usually acute to subacute, prominently nerved beneath, with conspicuous pale laminar glands. *Bracts* and *upper leaves* glandular-auriculate. *Sepals* and *bracts* with glandular-ciliate margin

Distribution of the species (see above) except Manipur and Myanmar. **CHINA.** [See also general distribution] **Guangxi**: Damiaoshan Xian, Yuanbaoshan, 21 October 1958 (fr), *Chun S.H.* 16863 (KUN). **Sichuan**: S. Wushan, n.d. (fl), *Wilson* 1389 (NY); Yuexi Xian, 3200 m, 31 August 1976 (fl & fr), *Sichuan Plant Exped.* 14230 (CDBI). **Yunnan**: au pied de Tsiang chan, au dessus de Ta-li, 2500 m, 25 September 1884, *Delavay* 189 (P); Menghwa [Weishan], Weipaoshan, 2300 m, 8 September 1933 (fl & fr), *Tsiang* 11386 (IBSC); Luoci Xian, Jiawoping, 2400 m, 23 October 1964 (fr), *Qiu B.Y.* 596341 (KUN). **Xizang**: W. of Yatung, 3000 m, 3 August 1936 (fl), *Spencer Chapman* 331 (K); Nyalam Xian, 2300 m, 13 August 1972 (fl), *Xizang Exped.* 1081 (PE); Cona Xian, 2700 m, 4 October 1974 (fr), *Qingzang Exped.* 74-2773 (KUN, PE).

INDIA. Meghalaya: Khasia, Lailankote, 1650 m, 28 November 1871(fr), *Clarke* 14795 (BM); **Arunachal Pradesh**: Dirong Dzong, 1500–1800 m, 4 August 1938 (fl), *Kingdon-Ward* 14043 (BM). **Benghal**: *Darjeeling, Lebong Cart Road, 1900 m, *Mukherjee A.* 1303 (CAL). **Sikkim**: Pemiongchi, 2100 m, 7 October 1875 (fr), *Clarke* 25094 (K); Changkyepyakop, 4200 m, 25 November 1911 (fr), *Ribu & Remee* 5718 (BM). **Uttar Pradesh**: Kumaon, Almora, 1500 m, n.d. (fl), *Strachey & Winterbottom* 2 (BM, GH, K); Tehri-Garhwal, below Mussoorie, 1950 m, September 1898, *Gamble* 27205 (K). **Himachal Pradesh**: Simla, Nugkunder, 2700 m, July 1885 (fl), *Collett* 763 (K); Dalhousie, 2100 m, 11 September 1874 (fl & fr), *Clarke* 22203 (BM). **Kashmir**: Basaoli [Basoli], 1800 m, 26 September 1876, *Clarke* 31607 (BM); Budrawan [Bhadrawan], 1800 m, 23 September 1876 (fr), *Clarke* 31503 (K).

BHUTAN. Central: Bumthang distr., Dhur, near Bumthang, 3000 m, 23 July 1949, *Ludlow, Sherriff & Hicks* 19503 (BM); Thimpu distr., Bele-da to Paro, 3600–2250 m, 9 July 1938, *Gould* 965 (K). **North**: Upper Mo Chu distr., Gasa Dzong, 2800 m, 14 September 1984 (fr), *Sinclair & Long* 4987 (E*, K).

NEPAL. East: Tinjure Danda, 2700 m, 7 September 1967 (fl & fr), *Williams & Stainton* 8408 (BM); Chauki, 2500 m, 17 August 1972 (fl), *Dobremez* 1510 (BM, GR*). **Central**: Godavari, Kathmandu Valley, 1590 m, 20 August 1965 (fl), *Schilling* 591 (K); Annapurna Himal, Siti Khola, 2100 m, 5 August 1954 (fl), *Stainton, Sykes & Williams* 6711 (BM). **West**: Bartadi, 1200 m, 29 July 1953 (fl), *Tyson* 135a (BM); Kaure/Sallyana, N. slope, 1560 m, 14 August 1969 (fl), *Flatt* 83 (BM).

The Yunnan specimens sometimes have rounded leaves, but they are much longer than those of subsp. *wardii*. One specimen from Bhutan (Chenkaphung, E. of Thimpu, *c.* 3000 m, 20 July 1979 (fl & fr), *Grierson & Long* 2798 (BM, E*)) is morphologically intermediate between *H. elodeoides* and *H. himalaicum* and would appear to be of hybrid origin.

4b. **Hypericum elodeoides** subsp. **wardii** N. Robson in *J. Jap. Bot.* **52**: 286 (1977); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 58 (1993). Type: Burma, Mt. Victoria, 2475–2700 m, 27 October 1956 (fl & fr), *Kingdon Ward* 22780 (BM!-holotype).
Fig. 13B, Map 10.

Leaves obtuse to rounded, not prominently nerved beneath, usually with obscure pale laminar glands. *Bracts* and *upper leaves* not glandular-auriculate. *Sepals* and *bracts* entire or subentire.

India (Manipur), Myanmar (Chin).
INDIA. Manipur: Sirhoi, 2400 m, 27 September 1948 (l. fl), *Kingdon Ward* 18113 (A, BM, NY*).

MYANMAR. Chin: Mt. Victoria, Esakan, 2100 m, 5 September 1956 (fl & e. fr), *Kingdon Ward* 22667 (BM).

The Manipur specimen is somewhat intermediate between the two subspecies in leaf characters and in sometimes (*Kingdon Ward* 18113 in A) having single glandular cilia on the sepals.

5. **Hypericum kingdonii** N. Robson, **stat. et nom. nov.** Type as for *H. wightianum* subsp. *axillare* N. Robson.
Map 10.

H. wightianum subsp. *axillare* N. Robson in *J. Jap. Bot.*: 287, ff. 3–4 (1977); Li Xiwen. in *Fl. Xizangica* **3**: 278, t. 113 ff. 1–2 (1986), in *Fl. R. P. Sinica* **50**(2): 57 (1990); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 80 (1993). Type: China, Xizang, Rima [Zayü], 1800 m, 27 August 1950 (fr), *Kingdon Ward* 29161 (BM!-holotype).

Icones: Li Xiwen in *Fl. Xizangica* **3**: 277, t. 113 ff. 1–2 (1986).

Perennial herb 0.15–0.48 m tall, suberect to decumbent from short rooting base, with stems usually branched from upper to nearly all nodes. *Stems* terete, eglandular; internodes 10–25 mm, longer than leaves. *Leaves* sessile, lower soon deciduous; lamina 6–14 × 3–7 mm, broadly ovate-oblong or broadly elliptic to suborbicular, pale or glaucous beneath, recurved, subchartaceous, apex rounded, margin entire, base shallowly cordate to rounded; venation: 3–4 pairs of main laterals from lower 2/5 of midrib, tertiary reticulation lax or apparently absent; laminar glands pale, punctiform, small, dense; intramarginal glands black, dense. *Inflorescence* 5–25-flowered from 1–2 nodes, usually with flowering branches from up to 6 nodes below and often also towards base of stem, the whole narrowly pyramidal to subcylindric; pedicels 1–2 mm; bracts and bracteoles narrowly elliptic or linear-lanceolate, black-glandular-denticulate to -fimbriate or subentire, with intercalary sessile black glands and ± well developed black-gland-fringed auricles, persistent. *Flowers* *c.* 8–14 mm in diam., stellate; buds ellipsoid, obtuse. *Sepals* 5, 4.5–6 × (1–)1.5–2 mm, equal, erect in bud and fruit, lanceolate to oblong-linear, acute to subacuminate, irregularly glandular-denticulate to -fimbriate or subentire; veins 3–5, branching; laminar glands pale, linear to punctiform and often a few black, punctiform; marginal or intramarginal glands black, irregular, often between glandular cilia or fimbriae. *Petals* 5, golden? yellow, not tinged red in bud, 6–8 × ? mm, *c.* 1.3–1.5 × sepals, narrowly ovate, acute, margin entire; laminar glands black, striiform to punctiform, sparse to rather dense; marginal glands distal and in apiculus, black. *Stamens* *c.* 20–25, '3'-fascicled, longest 5–6 mm, *c.* 0.7–0.85 × petals; anther gland black. *Ovary* 3-locular, *c.* 2 × 1 mm, ellipsoid; styles 3, *c.* 3 mm, 1.5 × ovary, ± divergent; stigmas narrow. *Capsule* 5–7 × 3.5–4.5 mm, narrowly ovoid to ellipsoid, *c.* 1.1 × sepals; valves with numerous lingitudinal vittae. *Seeds* yellow-brown, *c.* 0.5 mm, not carinate; testa finely scalariform. 2n = ?

Rice paddy bunds, grassy slopes; 1200–2700 m.

China (Xizang, Yunnan), Myanmar (Kachin), India (Arunachal Pradesh).

CHINA. Xizang: Bomi Xian, Tongmi Cun, 2000 m, 22 July 1965 (st), *Chang & Lang* 850 (PE); Zayu Xian, 1960 m, 29 July 1973 (fl & fr), *Qingzang Exped.* 73-932 (PE). **Yunnan**: Kiukiang Valley, Sochieh, 1700 m, 25 July 1938 (fl), *Yu T.T.* 19392 (PE).

MYANMAR. Kachin: Sources of the Irrawaddy, Adung Valley, 2100–2400 m, 31 March 1931 (fr), *Kingdon Ward* 9352 (BM); North Triangle, Uring Bum above Ahkail, 2700 m, 8 November 1953 (fr), *Kingdon Ward* 21570 (BM).

INDIA. Arunachal Pradesh: Delei Valley, 2100–2400 m, 15 August 1928 (fl), *Kingdon Ward* 8535 (K).

My original association of this taxon with *H. wightianum* was clearly wrong, as is shown by the dense, relatively large leaf laminar glands (characteristic of sect. *Elodeoida*, not of sect. *Monanthema*) and the larger flowers, which agree with those of *H. wightianum* essentially only in having sessile marginal glands in the sepals between the (irregular) glandular cilia. These sessile glands, however, are sometimes absent, resulting in an entire margin, which is unknown in *H. wightianum*. *H. kingdonii* is much better treated as a northern alpine relative of *H. elodeoides* subsp. *wardii*.

Sect. 9e. **MONANTHEMA** N. Robson, **sect. nov.**, sectioni 9. *Hyperico* similibus, sed caulis maturis teretibus vel ubi tenuibus 2–4(6)-lineatis, eglandulosis, bracteis bracteolisque glanduloso-ciliatis et auriculatis glandulosis instructis, inflorescentia 1–12-floribus, sepalis petalisque 5(4), petalis margine integris vel cilio glandulifero apicali unico instructis post anthesin deflexis vel patulis corrugatis, gynoecio (2)3(4)-meris, differt.

Hypericum sect. *Adenosepalum* sensu N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot.) **5**: 335 (1977) pro parte quoad *H. filicaule*.

Perennial herbs up to 0.4 m tall, with stems erect to prostrate, creeping and branching at base, glabrous, with dark (black or rarely red) glands on leaves, sepals, petals and anthers; branching lateral, from various nodes. *Stems* (mature) terete or (when slender) 2–4(6)-lined, eglandular or (4. *H. himalaicum* but very rarely) with few reddish glands on lines. *Leaves* opposite, decussate, sessile or to 3 mm pseudopetiolate, free, persistent; lamina entire or occasionally dark-glandular-ciliate, without or occasionally with gland-fringed auricles, with venation pinnate, closed and tertiary reticulation dense or very rarely rather dense to lax; laminar glands pale and/or black, punctiform to striiform, dense to almost absent, relatively small; ventral resin glands absent. *Inflorescence* 1–15(–*c.* 50)-flowered, with branching dichasial to monochasial from 1–2 nodes, sometimes with subsidiary branches from up to 4 nodes below; bracts and bracteoles gland-fringed and glandular-auriculate or entire and then usually foliar. *Flowers* stellate, homostylous. *Sepals* 5(4), free, persistent, erect in fruit, with margin glandular-ciliate to entire; veins 5–7(9), laminar glands pale and/or dark, linear to punctiform; marginal or submarginal glands black or reddish. *Petals* 5(4), persistent, deflexed to spreading, crumpling after flowering, with or without apiculus, margin entire or with apical glandular cilium; laminar glands pale and/or dark, linear to punctiform, and usually 1–4 sessile or subapical (immersed) dark glands. *Stamen fascicles* 5, united 2+2+1 (i.e. '3') or rarely 2+1+1+1 (i.e. '4'), persistent, with stamens totalling 10–45, filaments basally united; anther gland dark (black or rarely reddish); pollen type X. *Ovary* with (4)3(2) completely axile (or rarely incompletely axile to parietal) placentae, each ∞-ovulate; styles (4)3(2), free, divergent from discrete bases; stigmas narrow. *Capsule* (4)3(2)-valved, chartaceous to papyraceous, with valves longitudinally vittate. *Seeds* cylindric, not carinate or appendiculate; testa scalariform-reticulate to scalariform or foveolate.

BASIC CHROMOSOME NUMBER (X). Unknown.

HABITAT. Usually damp or wet, e.g. forest and woodland clearings, meadows, rocky or grassy slopes, marshes, bogs; 2100–4800 m.

DISTRIBUTION. South-west China (south Shaanxi, Sichuan, Yunnan, Xizang), Laos (north), Thailand (north), Myanmar (north), north India (Nagaland to Kashmir), Bhutan, Nepal, Pakistan, south India (Tamil Nadu), Sri Lanka.

7 species (+ 1 subspecies).

Key to sect. 9e. *Monanthema*

1 Sepal margin glandular-ciliate to entire, not glandular-denticulate; ovary and capsule 3-locular; sepals never with glands between glandular emergences 2

Sepal margin glandular-denticulate or ovary and capsule 1-locular; sepals often with sessile or intramarginal glands between glandular emergences 7

2(1) Capsule ovoid to subglobose; styles 1.5–3.5(–4) mm; uppermost leaf pair foliose, entire or with few basal stalked glands 3

Capsule ± ellipsoid or, if ovoid-ellipsoid to broadly ovoid, then styles 4–5 mm; uppermost leaf pair bracteose 5

3(2) Leaves (at least uppermost) sessile; sepals with pale laminar glandular lines or, if lines black, then margin glandular-ciliate; ovary ovoid to subglobose (1. **H. monanthemum**) 4

Leaves all shortly petiolate; sepals all with black linear laminar glands, entire; ovary ellipsoid ..... 2. **H. subcordatum**

4(3) Sepals and petals 5; sepals subequal, glandular-ciliate to subentire; flowers 12–25 mm in diam.; leaves 10–35 mm long ..... 1a. **H. monanthemum** subsp. **monanthemum**

Sepals and petals 4; sepals in unequal pairs, often foliose, entire; flowers 6–12 mm in diam.; leaves mostly 5–10 mm long ..... 1b. **H. monanthemum** subsp. **filicaule**

5(2) Styles 4–5 mm; capsule broadly ovoid; all leaves sessile, lamina oblong to triangular-ovate ..... 3. **H. trigonum**

Styles 2–3 mm; capsule ± ellipsoid; some or all leaves petiolate, lamina triangular-ovate to elliptic or oblanceolate to obovate 6

6(5) Stem (when mature) nearly always with long ± spreading branches from up to 5 nodes; styles equalling or shorter than ovary; sepals usually with black laminar glands ..... 4. **H. himalaicum**

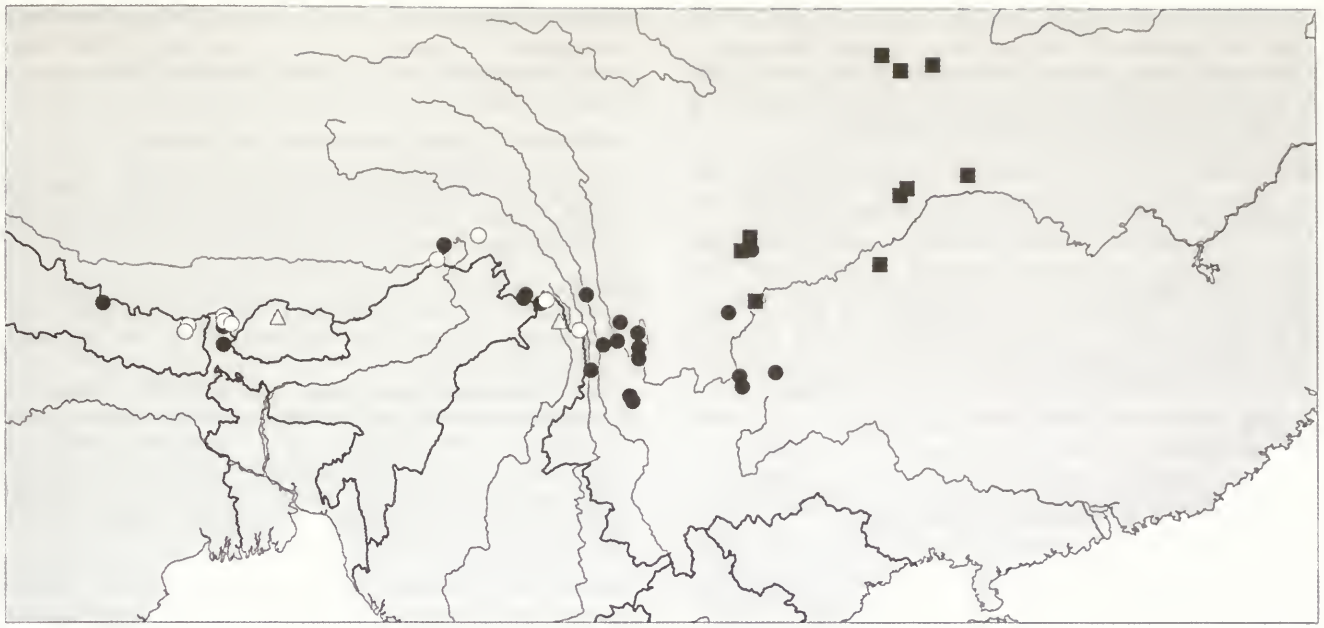
Stem unbranched below apical node or with a few short suberect branches; styles usually longer than ovary; sepals usually without black laminar glands ..... 5. **H. ludlowii**

7(1) Ovary and capsule ellipsoid to cylindric-ellipsoid; leaves all entire, sessile; sepals lanceolate to narrowly oblong-elliptic, glandular-denticulate ..... 6. **H. daliense**

Ovary and capsule subglobose to globose; leaves (at least upper) often glandular-ciliate, lower often pseudopetiolate; sepals broadly oblong or ± broadly elliptic, glandular-ciliate to glandular-laciniate ..... 7. **H. wightianum**

1. **Hypericum monanthemum** Hook. f. & Thoms. ex Dyer in Hook. f., *Fl. Brit. India* **1**: 256 (1874); Franchet in *Bull. Soc. Bot. France* **33**: 438 (1886); H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1904); N. Robson in Hara & Williams, *Enum. Fl. Pls Nepal* **2**: 62 (1979); Li Xiwen in *Fl. Xizangica* **3**: 276, excl. t. 114 ff. 3–6 (1986), in *Fl. R. P. Sinicae* **50** (2): 54, t. 10 ff. 8–13 (1990); Biswas in Sharma & Sanjappa, *Fl. India*, **3**: 69 (1993); Mukherjee & Chaudhri in *J. Econ. Taxon. Bot.* **20**: 126 (1996). Type: Sikkim, Lachen, 3300–3600 m, 12 July 1849 (fl & fr), *J.D. Hooker* s.n.

Fig. 14 A. *H. monanthemum* subsp. *monanthemum*: (a) habit; (b) sepal; (c) petal; (d) capsule. B. *H. monanthemum* subsp. *filicaule*: (e) habit; (f) sepal; (g) petal; (h) capsule; (i) small form, see note. C. *H. subcordatum*: (j) habit; (k) sepal; (l) petal; (m) capsule (young) (a, e, i, j × 2/3; rest × 6). A. (a) *Ludlow, Sherriff & Hicks* 20395, (b, c) *Forrest* 6136, (d) *Kingdon Ward* 9913A. B. (e–h) *Polunin* 1121, (i) *Kingdon Ward* 9882.



Map 11 Sect. 9e: 1a. *H. monanthemum* subsp. *monanthemum* ●; 1b. *H. monanthemum* subsp. *filicaule* ○ specimens, other records Δ; 2. *H. subcordatum* ■.

(K!-lectotype, selected here; GH!); Latong, 3450 m, 13 July 1849 (fl & fr), *J.D. Hooker* s.n. (K!-syntype).
Fig. 14A & B, Map 11.

Perennial herb (0.05)0.1–0.4 m tall or long, erect or decumbent to prostrate from creeping, rooting and branching base, with stems scattered or clustered or often carpeting, often slender, unbranched above or rarely with one pair of ascending branches below inflorescence. *Stems* terete or 2(4)-lined, eglandular; internodes 5–50 mm, longer than leaves. *Leaves* sessile (uppermost or very rarely all) or to 1 mm petiolate, lower smaller, erect to appressed, soon deciduous; lamina 4–25(–35) × 2–15(–25) mm, broadly ovate or circular to broadly oblong or broadly elliptic or obovate-spathulate, paler or slightly glaucous beneath, plane, subchartaceous to submembraneous; apex rounded or retuse to obtuse, margin entire, plane, base rounded to truncate or subcordate or (lower) cuneate; venation 3(4) pairs of main laterals from lower third of midrib, with tertiary reticulation dense; laminar glands punctiform, all pale and very small or some or all black; intramarginal glands black and dense or reddish to pale and rather sparse. *Inflorescence* 1–5(–7)-flowered, from 1(2) nodes, subumbelliform or bifurcate; pedicels 0.5–2.5 mm (–5 mm in central flower); bracts foliaceous, the pair usually wider than inflorescence, entire; bracteoles narrowly ovate to lanceolate, black-glandular-ciliate and -auriculate, persistent. *Flowers* (6–)10–25 mm in diam., stellate to reflexed; buds narrowly ovoid, obtuse. *Sepals* 5, subequal or 4 in unequal pairs, erect in bud and fruit, 2.5–7 × 1–3 mm, oblong or elliptic to narrowly ovate or linear-lanceolate, obtuse (rarely acute) to rounded, glandular-ciliate to entire; veins 5–7, branching and often reticulating towards margin; laminar glands all pale or parts or all black, linear; marginal glands black, on cilia or sessile, or reddish to pale, sessile or intramarginal. *Petals* 5–4, golden yellow, not tinged red in bud, (3) 5–15 × 1–4.5 mm, 1–2 × sepals, lanceolate-oblong to narrowly ovate, obtuse to acute, margin entire, laminar glands few, pale or black, linear to striiform, or absent, apiculus gland reddish, other marginal glands absent. *Stamens* 10–45, '3'-fascicled, longest *c.* 4–9 mm, 0.6–0.8 × petals; anther gland black. *Ovary* (4?)3(2?)-locular 2–5 × 1.5–2.5 mm, ovoid to subglobose; styles (4)3(2), 1.5–3.5(–4) mm, 0.5–1 × ovary; stigmas narrow. *Capsule* (5–)6–8 × (3–)4–6 mm, broadly ovoid-ellipsoid to ellipsoid; valves with numerous longitudinal vittae. *Seeds* yellowish brown, 0.7–0.8 mm, cylindric, acute at both ends; testa shallowly foveolate. 2n = ?

Clearings in forests and bamboo forests, thickets, grassy or stony slopes and streamsides, rock crevices; 2270–4400(–4800) m.

Himalayan Range from west Sichuan and Yunnan to Nepal.

Joseph Hooker collected two similar plants in Sikkim, one with a 5-merous perianth and the other with a 4-merous perianth. Thistleton Dyer (1874) placed the former in *Hypericum* (*H. monanthemum*) and the latter along with other 4-merous *Hypericum* relatives in the Linnaean genus *Ascyrum* (*A. filicaule* Dyer), even though all previously described *Ascyrum* species had been shrubs or herbaceous derivatives from eastern North America and the Caribbean. In addition, *A. filicaule* has black anther glands, whereas all the American plants are completely destitute of black glands. The Himalayan plant would therefore seem to have developed 4-mery independently.

A detailed study has revealed that not only is *A. filicaule* a *Hypericum*, but also that it is only with difficulty separable from *H. monanthemum*. This latter 'species' displays a western reduction trend, from China to Nepal, while the reduction trend in *A. filicaule* goes in the reverse direction, from Nepal and Sikkim to Yunnan and Myanmar. In Nepal, Sikkim and Bhutan there is an area of morphological overlap, where some specimens have perianth states intermediate between 5-mery and 4-mery. It therefore seems appropriate to treat these taxa as subspecies.

1a. **Hypericum monanthemum** subsp. **monanthemum**
Fig. 14A, Map 11.

H. monanthemum var. *nigropunctatum* Franchet, *Pl. delavay.*: 103 (1889) ['*nigro-punctatum*']. Type: China, Yunnan, in locis umbrosis montis Tsang-chan, supra Tali, 4000 m, 3 August 1884 (fl), *Delavay* 1944 (P!-holotype; K!-isotype).

H. yunnanense Franchet in *Bull. Soc. Bot. France.* **54**: 437 (1886) pro parte quoad specc. *Delavay* 93 et 1941.

H. mairei H. Léveillé in *Bull. Acad. Int. Géogr. Bot.* **25**: 23 (1915) non H. Léveillé (1912). Type: China, Yunnan, pâturages du plateau de Ta-Hai, 3200 m, July 1912, *Maire* s.n. (E-holotype).
H. bachii H. Léveillé, *Cat. Pl. Yun-nan*: 131 (1916). Type as for *H. mairei* H. Léveillé (1915) non H. Léveillé (1912).

Icon: Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 53, t. 10 ff. 8–13 (1990).

Plant erect. *Stems* terete. *Leaves* sessile or subsessile, 10–25(–35) × 8–15(–25) mm, never scale-like, subchartaceous, sometimes slightly glaucous beneath, base rounded to broadly cuneate, intramarginal glands black. *Inflorescence* 1–5(–7)-flowered, pedicels 1–2.5 mm. *Flowers* 12–25 mm in diam. *Sepals* 5, subequal, 4–7 × 1.5–3 mm, margin glandular-ciliate to subentire. *Petals* 5, 8–15 × 2.5–4.5 mm, *c.* 2 × sepals. *Stamens* 20–45. *Styles c.* 0.6–1 × ovary.

Clearings in forests and bamboo forests, grassy slopes, streamsides; 2270–*c.* 4000 m.

China (west Sichuan, Yunnan, south-east Xizang), Myanmar (Kachin), Bhutan, India (Benghal, Sikkim), Nepal.
CHINA. Sichuan: Emei Shan, 3300 m, 25 July 1931 (fl & fr), *Tang & Wang* 23435 (GH, KUN, NAS); Ebian Xian, 2600 m, 25 July 1976 (fl), *Sichuan Pl. Exped.* 13188 (CDBI). **Yunnan**: Dali Xian, Diancang Shan, 2900–3200 m, 19 July 1984 (fl & e. fr), *Sino-Amer. Bot. Exped.* 1166 (A, BM, CAS, KUN, US); Lichiang Range, E. flank (27° 30¢ N), 3300 m, July 1910 (fl), *Forrest* 6136 (BM, E*, K); Chih-tze-lo Hsien, Pi-lo Shan, 4000 m, 27 August 1934 (fr), *Tsai H.T.* 58243 (A, IBSC, KUN, PE). **Xizang**: Zayu Xian, 3600 m, 13 August 1973 (fl), *Qingzang Exped.* 73-1083 (KUN, PE); Kongbo Prov., Tumbatse, Rong Chu, 3480 m, 2 July 1938 (fl), *Ludlow, Sherriff & Taylor* 5093 (BM); Yatung, 27° 51¢ N, 88° 35¢ E, 1897 (fl & fr), *Hobson* s.n. (K).
MYANMAR. Kachin: Nam Tamai valley (Adung Wang–Gamlang Wang), 3000–3600 m, 1 October 1937 (fl), *Kingdon Ward* 13344 (BM); Adung valley, sources of the Irrawaddy, 3600 m, 8 August 1931 (fl & fr), *Kingdon Ward* 9763 (BM).
BHUTAN. North: Me La, 3900 m, 23 June 1949 (fl), *Ludlow, Sherriff & Hicks* 20395 (BM, E*); Upper Pho Chu (east branch), Leji, 3600 m, 28 June 1949 (fl), *Ludlow, Sherriff & Hicks* 16671 (BM, E*).
INDIA. Benghal: *Tonglu, 3000 m, *Smith & Cave* 2537 (Lloyd Bot. Gdn, Darjeeling). **Sikkim**: Theumthang [Thaunthang], 4050 m, 2 August 1913 (fl), *Cooper* 408 (BM, E*); Lachen, 3300–3600 m, 12 July 1849 (fl & fr), *Hooker* s.n. (GH, K).
NEPAL. East: Topke Gola, 3450 m, 4 July 1971 (fl), *Beer* 8271 (BM).

The Cooper (Sikkim) and Beer (Nepal) specimens are intermediate between subspp. *monanthemum* and *filicaule*.

1b. **Hypericum monanthemum** subsp. **filicaule** (Dyer) N. Robson, **comb. et stat. nov.** Type as for *Ascyrum filicaule* Dyer.
Fig. 14B, Map 11.

Ascyrum filicaule Dyer in Hook. f., *Fl. Brit. India* **1**: 252 (1874); Li Xiwen in *Acta Bot. Yunnan.* **3**: 329, ff. 1.4, 1.5 (1981). Type: India, Sikkim, Lachoong Valley, 3600 m, 3 September 1849 (fl), *J. D. Hooker* s.n. (K!-holotype).
Hypericum filicaule (Dyer) N. Robson in *Bull. Br. Mus. nat. Hist.* (Bot). **5**: 305 (1977); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 52, t. 10 ff. 1–7 (1990); Biswas in Sharma & Sanjappa, *Fl. India*, **3**: 58 (1993).

Icon: Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 53, t. 10 ff. 1–7 (1990).

Plant erect to decumbent or prostrate and ± mat-forming, with stems unbranched above or (in Yunnan) branched from upper 2–3 nodes. *Stems* terete or narrowly 2-lined. *Leaves* to 1 mm petiolate, (4–)5–10(–15) × 2–8(–11) mm, broadly elliptic, lower gradually smaller, sometimes becoming minute and scale-like, thinly chartaceous to membranous, paler beneath, base cuneate to rounded-attenuate, intramarginal glands reddish or pale. *Inflorescence* 1-flowered, pedicels (terminal) 0.5–1.5 mm. *Flowers* 6–12 mm in diam. *Sepals* 4, sometimes foliar, outer 4–12 × 1.5–7 mm, inner 3–7 × 1–3 mm, obtuse, margin entire. *Petals* 4, 3–8 × 1–2.7 mm, 0.75 –1.6 × sepals. *Stamens* 10–20. *Styles* 0.5–0.8 × ovary.

In rock crevices and on grassy slopes; 3000–4800 m.

China (north-west Yunnan, south-east Xizang), India (Arunachal Pradesh, Sikkim), Nepal and possibly Myanmar (see note below).
CHINA. Yunnan: Gongshan Xian, Longpanla, 3500 m, October 1935 (st), *Wang C.W.* 67066 (KUN); loc. not stated, 1917–1919 (st), *Forrest* 14279 (BM, E*). **Xizang**: Bomi Xian, 4000 m, 15 August 1965 (fl), *Ying & Hong* 651164 (PE); ? Xian, Chickchor, 3600 m, 5 July 1935 (fl), *Kingdon Ward* 11899 (BM); Kongbo Prov., Lusha Chu, 3600 m, 8 June 1938 (fl), *Ludlow, Sherriff & Taylor* 4713 (BM).
INDIA. Arunachal Pradesh: Senge Dzong, 3600–3900 m, 30 May 1935 (fl), *Kingdon Ward* 11561 (BM); Bhutan frontier, Orka La, 3900 m, 12 June 1938 (fl), *Kingdon Ward* 13728 (BM). Sikkim: Lachen, 3600 m, 20 June 1849 (fl), *Hooker* s.n. (K); Lachoong, 3600 m, 3 September 1849 (fl), *Hooker* s.n. (K).
NEPAL. Central: Rambrong, Lamjung Himal, 4050 m, 7 July 1954, *Stainton, Sykes & Williams* 6216 (BM); Khola Kharka, c. 4050 m, 17–19 July 1949 (fl), *Polunin* 1121 (BM).

Subsp. *filicaule* almost certainly occurs in Bhutan.

NOTE. An extremely reduced form of subsp. *filicaule* was collected by Kingdon Ward in the same region of north Myanmar as that in which he found plants of subsp. *monanthemum*. I am reluctant to describe it as a distinct taxon in the absence of other similar material from Myanmar or adjacent Yunnan or Xizang, as it differs essentially from some Chinese populations (e.g. *Feng* 6550) only in size of parts and occurs in a region very close to the Xizang part of the range of subsp. *filicaule*:

Herb 'forming mossy clumps on granite boulders', with stems prostrate to ascending, branching distally. *Stems* filamentous, eglandular, narrowly 4-lined, becoming 2-sided; internodes 1.5–3 mm, upper exceeding leaves, lower shorter than them. *Leaves* all with petioles 0.2–0.3 mm; lamina broadly ovate to orbicular, upper 2–4 × 1.5–3 mm, decreasing in size towards base, subappressed, outcurving, paler beneath; apex rounded, margin entire, base cuneate to angustate; veins: 3 pairs of laterals from lower third, tertiary reticulation lax; laminar glands pale rather sparse; marginal glands very small, pale, spaced. *Inflorescence* 1-flowered. *Flowers c.* 8 mm in diam., stellate; buds narrowly ellipsoid. *Sepals* 4, unequal, 2 × 1.2 (outer) or 0.6 (inner) mm, elliptic to oblanceolate, entire, rounded; laminar glands pale, punctiform to striiform; marginal glands absent. *Petals* 4, 'yellow', 5–5.5 × 1.5–2 mm, *c.* 2.5 × sepals, oblong, almost entire; laminar glands absent, marginal gland solitary, terminal, on short cilium, reddish. *Stamens* 12, '3'-fascicled with 4 in each fascicle, longest 2.5–3 mm, *c.* 0.5 × petals; anther gland black. *Ovary* 1-locular, *c.* 1.5 × 1 mm, narrowly ovoid; styles 3, 0.9–1.1 mm, *c.* 0.65 × ovary; stigmas purple, narrowly capitate. *Capsule* 2.5–3.5 × 2–2.5 mm, ellipsoid; valves finely vittate. *Seeds* yellow-brown, *c.* 0.5 mm, cylindric; testa shallowly finely scalariform.

MYANMAR. Kachin: Adung Valley, sources of the Irrawaddy, 3900–4200 m, 31 March 1931 (fl & fr), *Kingdon Ward* 9882 (BM).

2. **Hypericum subcordatum** (R. Keller) N. Robson, **comb. et stat. nov.** Type as for *H. thomsonii* var. *subcordatum* R. Keller.
Fig. 14C, Map 11.

H. thomsonii var. *subcordatum* R. Keller in *Bot. Jb.* **33**: 553 (1904). Type: China, Shaanxi, Huan-tou-san, July 1899 (fl & fr), *Giraldi* 540 (FI-holotype).
H. thomsonii R. Keller in *Bot. Jb.* **33**: 552 (1904) pro parte excl. typum.

H. mororanense R. Keller in *Bot. Jb.* **33**: 552 (1904) pro parte quoad spec. Sin. cit.

H. petiolulatum var. *subcordatum* (R. Keller) H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908).

Perennial herb 0.1–0.17 m tall, erect from creeping and rooting base with stems unbranched or branched from upper 1(2) nodes. *Stems* slender, eglandular; internodes 2-lined above, terete below, 30–40 mm, longer than leaves. *Leaves* all petiolate, with petiole 1–1.5 mm; lamina 10–16 × 8–12 mm, broadly elliptic or oblong-elliptic to obovate, paler (or subglaucous?) beneath; apex rounded, margin entire, base cuneate to truncate (or uppermost subcordate); veins: 3 pairs of laterals from lower third or lower, tertiary reticulation rather dense, obscure; laminar glands dense, small, pale or sometimes a few black, scattered; marginal glands dense or subirregular, black. *Inflorescence* (1–)3–5-flowered, occasionally with branches from 1(2) nodes below, the whole corymbiform or bifurcating to subcylindric; pedicels 2–2.5 mm; bracts and bracteoles foliar, entire. *Flowers c.* (8–)10–12 mm in diam., stellate; buds ellipsoid? *Sepals* 5, subequal, 3–4.5 × 0.8–1.2 mm, oblong-lanceolate to lanceolate, acute, margin entire; veins 5, unbranched; laminar glands linear to (distally) punctiform, black; marginal glands few, sessile or submarginal, all or most distal, black. *Petals* 5, golden? yellow, 4.5–6 × 1–1.5 mm, 1.35–1.5 × sepals, narrowly elliptic, entire, laminar glands few, black, linear to striiform, marginal glands few, black, subapical or absent. *Stamens* 17–20, '3'-fascicled, longest 4–5.5 mm, *c.* 0.9 × petals; anther gland black. *Ovary* 3(4)-locular *c.* 2 × 1 mm, ellipsoid; styles 3(4), *c.* 1.7–2 mm, *c.* 0.85–1 × ovary, narrowly or scarcely capitate. *Capsule* 4.8–6 × 3.5–4 mm, ovoid to subglobose; valves densely longitudinally vittate. *Seeds* yellow-brown, 0.6 mm, cylindric; testa shallowly finely scalariform. 2n = ?

No habitat details known; 1800–2850 m.

China (Shaanxi, Sichuan).

CHINA. Shaanxi (south): Cho-toc Miao, Hu Shien, n.d. (fl), *Fr Hugh [Scallan]* s.n. (BM); Mt Thae-pei-san, August 1899 (fr), *Fr Hugh* s.n. (BM); Taibai Shan, Lotosze, 1800 m, 21 September 1932 (fr), *Hao K. S.* 4303 (PE); Taibai [Thae-pei] Shan, Pingan Si to Fangyang Si, 11 September 1937 (fr), *Liou & Tsoong* 817 (PE); Taibai Shan, Fangyang Si to Mingqing Si, 2850 m, 11 August 1977 (fl & fr), *Guo & Hu* 525 (IBSC); Huan-tou-san, July 1899 (fl & fr), *Fr Hugh* s.n. (BM); Mt Miao-Wang-san, 1898 (fr), *Fr Hugh* s.n. (BM); Wu Shan, summit, 1 July 1903 (fl), *Wilson* 3259 (K). **Sichuan**: Emei Shan, 2300 m, 24 June 1940 (fl), *Ma W.W.* 2606 (KUN, US); Ebian Shan, Shouping Shan, 25 August 1939 (fr), *Shang (Sun?) S.S.* 1063 (A, KUN, US); Hongya Xian, Wawu Shan, 1 July 1939 (fl), *Yao C.W.* 3978 (PE); Nanchuan Xian, Jin Shan, 1980 m, 1 July 1957 (fr), *Tsuing & Zhou* 92391 (IBSC); Leibo Xian, 2400 m, 23 June 1959 (fl), *Kuan C.T.* 7635 (IBSC); Wuxi Xian, Shuanggou Xiang, 2600 m, 23 July 1958 (fl & fr), *Yang G.H.* 58939 (PE).

H. subcordatum is very closely related to *H. monanthemum* subsp. *monanthemum* and continues the northward trend of that taxon. Indeed, it could be regarded as a small delicate 'form' of *H. monanthemum* var. *nigropunctatum* (i.e the form of the type subspecies with black-gland-lined sepals) except that the leaves are all petiolate and the sepals acute and entire, characters that do not occur in combination in *H. monanthemum* itself. These differences, together with the occurrence of both taxa on Emei Shan, where they remain distinct, would appear to justify the separation of *H. subcordatum* as a species.

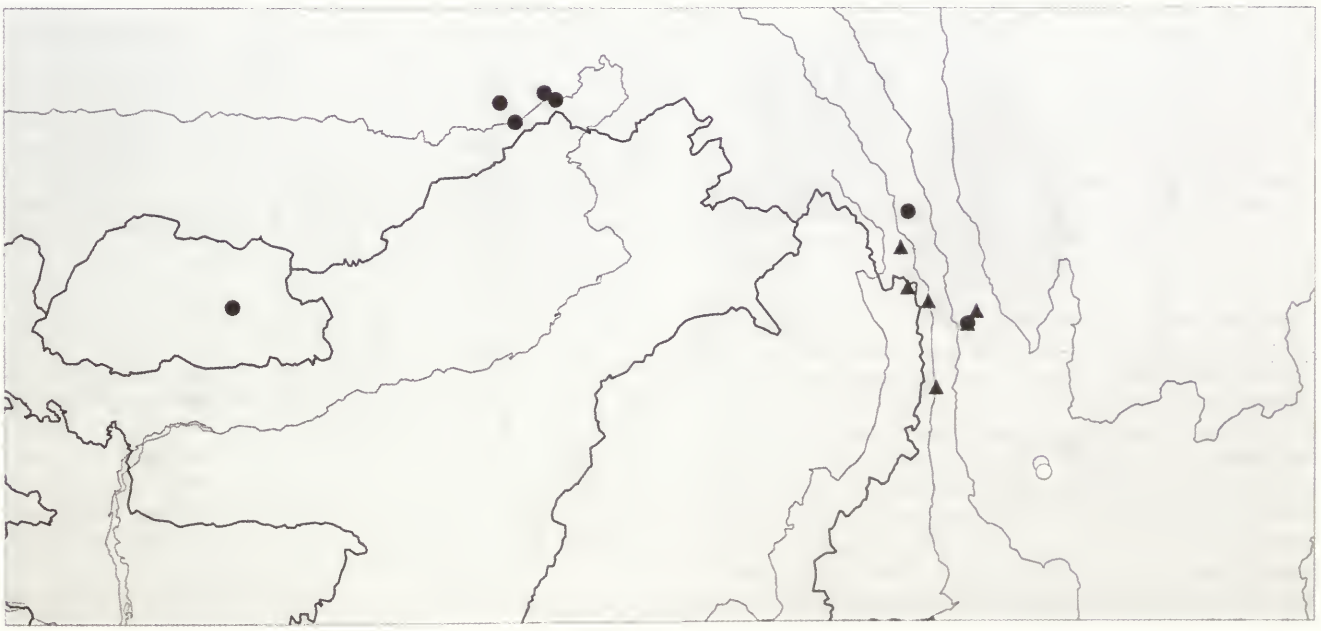
3. **Hypericum trigonum** Hand.-Mazz., *Symb. Sin.* **7**: 403, t. 8 f. 6 (1931). Type: China, Yunnan (NW), 'am Passe Akelo zwischen Djinscha-djiang ("Yangtse") und Landsang-djiang (Mekong), 27° 19′, am Wege von Djitsung nach Kakatang', 2900–3100 m, 30 August 1915 (fl & fr), *Handel-Mazzetti* 7920 (W!-holotype; US!-isotype).

Fig. 15A, Map 12.

H. monanthemum sensu Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 276 (1990) pro parte excl. typum.

Icon: Hand.-Mazz., *Symb. Sin.* **7**: 403, t. 8 f. 6 (1931).

Perennial herb 0.25–0.4 m tall, erect from short creeping and rooting base, with stems unbranched below inflorescence or with slender ascending or spreading branches from up to *c.* 5 upper nodes. *Stems* terete, eglandular; internodes 20–43 mm, longer than or equalling leaves. *Leaves* sessile, lower not smaller but ascending



Map 12 Sect. 9e: 3. *H. trigonum* ▲; 5. *H. ludlowii* ●; 6. *H. daliense* ○.

Fig. 15 A. *H. trigonum*: (a) habit; (b) sepal; (c) petal; (d) capsule (young). B. *H. himalaicum*: (e) habit; (f) sepal; (g) petal; (h) capsule. C. *H. ludlowii*: (i) habit; (j) habit, small form; (k) sepal; (l) petal; (m) capsule (a, e, i, j × 2/3; rest × 6). A. *Kingdon Ward* 9913. B. *Stainton, Sykes & Williams* 1666. C. (i, k, l) *Ludlow, Sherriff & Taylor* 5461, (j) *Ludlow, Sherriff & Hicks* 19502, (m) *Ludlow & Sherriff* 14214.

and soon deciduous; lamina 20–30 × 9–15 mm, oblong or oblong-ovate to triangular-ovate, paler beneath, not glaucous, plane, subchartaceous; apex rounded to obtuse, margin entire, base broadly cuneate to shallowly cordate; venation: 4 pairs of main laterals from lower half of midrib, with tertiary reticulation dense; laminar glands punctiform, all pale and very small or all black; intramarginal glands black, dense. *Inflorescence* 4–*c.* 15-flowered from terminal node, with flowering branches from up to 4 nodes below, the whole corymbiform to cylindric; pedicels 1–2.5(–5, central flower) mm; bracts narrowly lanceolate to linear, black-glandular-ciliate and -auriculate (cilia long), persistent. *Flowers* 15–*c.* 25 mm in diam., stellate or reflexed; buds cylindric, rounded. *Sepals* 5, equal, erect in bud and fruit, 6–7 × 1.5–2 mm, narrowly oblong to elliptic-oblong or lanceolate, acute, glandular-ciliate; veins 5, branching and sometimes reticulating towards margin; laminar glands all pale or parts black, linear or interrupted; marginal glands black, on cilia. *Petals* 5, golden yellow, not tinged red in bud, 9–11 × 2.5–4.5 mm, *c.* 1.5(–2?) × sepals, narrowly oblong-elliptic to lanceolate-elliptic, acute (i.e. with prominent apiculus), margin entire, laminar glands few, pale, linear and sometimes black, 1–3, subapical; marginal gland solitary, in apiculus, black. *Stamens c.* 25–35, '3'-fascicled, longest 7–9 mm, *c.* 0.75–0.8 × petals; anther gland black. *Ovary* 3-locular?, *c.* 4–5 × 1.8–2 mm, narrowly ovoid-ellipsoid; styles 3, 4–5 mm, about equalling ovary; stigmas narrowly capitate. *Capsule* 7–8 × *c.* 4.5 mm, broadly ellipsoid, *c.* 1–1.5 × sepals; valves with numerous longitudinal vittae. *Seeds* not seen. 2n = ?

Marshes and wet meadows?; 2600–3650 m.

China (north-west Yunnan).

CHINA. Yunnan: Jugo-shan Pass, 3600 m, 30 June 1922 (fl), *J.W. & C.J. Gregory* s.n. (BM); Litiping between Likiang and Weihsi, 8 October 1939 (fr), *Ching R.C.* 22069 (A, KUN); Weixi Xian, Yezhi, 3650 m, 6 October 1934 (fr), *Tsai H.T.* 59699 (A, IBSC, KUN, NAS, PE); Gongshan Xian, 9 October 1940 (fr), *Feng K.M.* 8308 (KUN); Mekong-Salwin Divide, Sila, 3400 m, 25 September 1928 (fl & fr), *Yu T.T.* 22728 (A).

The *H. trigonum* group (Spp. 3–5), with the closely allied *H. monanthemum* group (Spp. 1–2), would appear to be related to *H. przewalskii* and to be derived from it along with, but independently of, the *H. seniawinii* group (sect. *Elodeoida*) (see p. 46). Although members of both groups have penetrated westward along the Himalayan Range, the *H. seniawinii* group is basically south-eastern and upland and the montane species are derivative. The *H. trigonum* group, on the other hand, is basically south-western and montane. Both groups contain variable taxa that are sometimes difficult to separate specifically, but *H. trigonum* and its relatives are particularly complex in this regard. The group comprises *H. trigonum* (north-west Yunnan), *H. himalaicum* (Pakistan to north-west Yunnan and adjacent Sichuan) and *H. ludlowi*i (Yunnan, south-east Xizang and Bhutan). *H. trigonum* is basic to the group, being most similar to the long-styled form of *H. monanthemum*, and the two other taxa are apparently derived from it. The problem is to decide whether there are three species or one species with three subspecies or something in between. The decision is complicated by a population in extreme northern Myanmar and adjacent Arunachal Pradesh that is intermediate in some respects between *H. trigonum* and *H. himalaicum*. Short of making four subspecies, which would not, I think, be a satisfactory reflection of the situation, it seems best to recognize three species and place the intermediate population in *H. himalaicum*, despite the long distance between its range (Arunachal Pradesh–Myanmar frontier) and that of the most primitive form of *H. himalaicum* proper (central Nepal).

4. **Hypericum himalaicum** N. Robson in *J. Jap. Bot.* **52**: 287, ff. 3–4 (1977), in Hara & Williams, *Enum. Fl. Pls Nepal* **2**: 61 (1979); Robson & Long in Grierson & Long, *Fl. Bhutan* **1**(2): 377, f. 30e–g (1984); Li Xiwen in *Fl. Xizangica* **3**: 278 (1986), in *Fl. R. P. Sinicae* **50**(2): 56 (1990) pro parte uterque quoad typum; Biswas in Sharma & Sanjappa, *Fl. India*, **3**: 64 (1993); Mukherjee & Chaudhuri in *J. Econ. Taxon. Bot.* **20**: 125 (1996). Type: Nepal, Gossain Than, n.d. (fl), *Wallich* 4814 (K-W!-holotype; BM!, K!-isotypes).

Fig. 15B, Map 13.

H. pallens D. Don, *Prodr. fl. nepal.*: 219 (1825), nom. illegit. superfl. pro parte excl. typum, non *H. pallens* Banks & Solander (1794).

H. setosum Wall. [*Num. List*: no. 4814 (1831), nomen] ex Dyer in Hook. f., *Fl. Brit. India* **1**: 256 (1874) in syn., non *H. setosum* L. (1753).

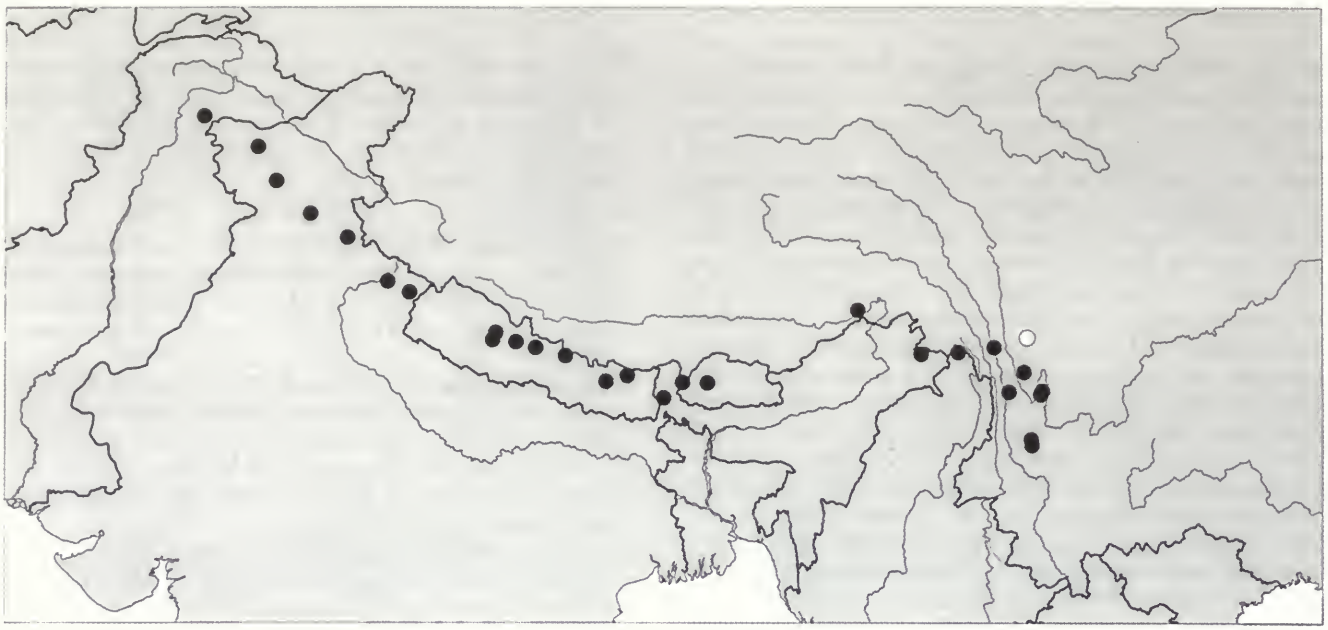
H. napaulense sensu Dyer in Hook. f., *Fl. Brit. India* **1**: 256 (1874) pro parte excl. typum; Y. Kimura in Kihara, *Fauna & Fl. Nepal Himal.*: 278 (1955); Anon. in *Bull. Dept. Med. Pl., Thapathali* **1**: 7 (1967); N. Robson in Nasir & Ali, *Fl. W. Pakistan* **32**: 11, f. 2A–F (1973) pro parte excl. syn. *H. monanthemum*; pro parte omnes excl. typum.

H. monanthemum var. *brachypetalum* Franchet, *Pl. delavay.*: 104 (1889). Type: China, Yunnan, in pratis ad collum Yen-tze-hay, 3200 m, 17 June 1887 (fl), *Delavay* 5180 (P!-lectotype, selected here; K!-isolectotype); Yunnan, in collibus prope Pien-kio, 11 November 1887 (fl), *Delavay* s.n. (P!-syntype).

H. humifusum sensu Y. Kimura in Hara, *Fl. E. Himal.*: 209 (1966).

Icones: N. Robson in *Fl.W. Pakistan* **32**: 11, f. 2A–F (1973), in *Fl. Bhutan* **1**(2): 377, f. 30 e–g (1984).

Perennial herb 0.05–0.35 m tall or long, suberect to decumbent from creeping and rooting base, with stems solitary? or clustered, often branched below inflorescence or lower, with branches slender, spreading. *Stems* terete or 2–4(6)-lined, eglandular or occasionally with few reddish glands on lines; internodes 8–50 mm, longer than leaves. *Leaves* sessile or to 2 mm petiolate; lamina 4–24 × 2–17 mm, ovoid to oblong or elliptic to obovate or oblanceolate, paler or usually glaucous beneath, plane, subchartaceous; apex rounded, margin entire, base cordate to rounded or cuneate, the upper often with black-glandular-ciliate auricles and sometimes also glandular-ciliate proximal margin; venation: 2–4 pairs of main laterals from lower quarter to almost half of midrib, with tertiary reticulation dense; laminar glands pale, punctiform, small to medium, dense; intramarginal glands black, dense. *Inflorescence* 1–12-flowered, from 1(2) nodes, often with flowering branches from up to 4 nodes below, the whole subcorymbiform; pedicels 1.5–4 mm; bracts and bracteoles narrowly elliptic or linear-lanceolate to linear, black-glandular-ciliate and -auriculate or more rarely entire and then either bracteose or reduced-foliar, persistent. *Flowers* 10–20 mm in diam., stellate; buds ovoid to broadly ellipsoid, obtuse to acute. *Sepals* 5, 3.5–7 × 1–2.5 mm, equal to subequal, erect in bud and fruit, ovate-lanceolate or elliptic to linear-lanceolate, subacute to acute or rarely rounded, glandular-ciliate to entire; laminar glands pale or often partly black, linear (with black parts dots to usually streaks) to dots; marginal glands black, on cilia or sessile or absent. *Petals* 5, bright yellow, sometimes tinged red in bud, 6–10 × 2–4 mm, 1.2–2 × sepals, oblong-elliptic to oblanceolate, rounded, margin entire or rarely with one apical glandular cilium, laminar glands black, striiform, or absent, marginal glands absent or 1–4, black, apical and subapical, sessile or apical on cilium. *Stamens* 12–30, '3'-fascicled, longest 4–7 mm, 0.65–0.85 × petals; anther gland black. *Ovary* 3-locular, 2–3.5 × 1.5–2 mm, ovoid to ellipsoid; styles 3(4), 2–3 mm, 0.65–1(–1.3?) × ovary; stigmas narrowly capitate to narrow. *Capsule* 3–9 × 2.5–6 mm, ± broadly ellipsoid, exceeding or equalling sepals. *Seeds* yellowish-brown, 0.5–0.6 mm, cylindric; testa densely scalariform-foveolate. 2n = ?



Map 13 Sect. 9e: 4. *H. himalaicum* ● specimens, other record ○.

Forest and woodland clearings, alpine meadows and rocky or grassy slopes, often in damp places; 2100–3900 m.

Himalaya from Pakistan to east Bhutan and China (south-east Xizang, west Yunnan and adjacent? Sichuan), with an isolated population in the Arunachal Pradesh–Myanmar frontier area (see note under 3. *H. trigonum*).

CHINA. Sichuan: no precise locality, 3150 m, 9 August 1964 (fl & fr), *Sichuan Exped.* 04053 (CDBI). **Yunnan**: E. flank of Lichiang Range, 27° 30¢, 3300 m, July 1910 (fl), *Forrest* 6016 (BM, K); Zhongdian Xian, 3200 m, 28 August 1962 (fl), *Zhongdian Exped.* 1598 (KUN, PE); Yangbi Xian, W. side of Diancang Shan, vicinity of Dajiuping, 2500–2600 m, 30 June 1984 (fl), *1984 Sino-Amer. Bot. Exped.* 620 (A, BM, CAS, KUN, US). **Xizang**: Nage, 3200 m, 31 July 1974 (fl & fr), *Qingzang Exped.* 74-3797 (PE); Nyingchi Xian, 3040 m, 28 July 1965 (fr), *Chang & Lang* 1024 (PE); Yadong Xian, 3100 m, 15 September 1974 (fl & fr), *Qingzang Exped.* 74-2561 (KUN, PE).

MYANMAR. Kachin: Sources of the Irrawaddy, Adung Valley, 3600 m, 7 August 1931 (fl), *Kingdon Ward* 9913 (BM).

INDIA (East). Arunachal Pradesh: Assam frontier, Mishmi Hills, Delei Valley, Dri La, 3000 m, 13 December 1933 (fr), *Kingdon Ward* 11049 (BM). Benghal: Kalimpong, Labah, 2100 m, September 1904 (fr), *Haines* B.B. 983 (K); Darjeeling [Därjiling], Singaleleh, 3000 m, 7 October 1870 (fr), *Clarke* 13513 (K). **Sikkim**: Tonglo, 3000 m, 5 August 1874 (fl), *Treutler* 505 (K); Jongri, 3600 m, 15 October 1875 (fr), *Clarke* 25852 (K).

BHUTAN. Central: Thimpu [Thimbu) distr., E. of Thimphu, *c.* 3000 m, 20 July 1979 (fl), *Grierson & Long* 2798 (BM, E*).

NEPAL. East: Kasuwa Khola, 3450 m, 18 August 1975 (fl & fr), *Beer* 25327 (BM); Lumding Khola, 3000 m, 13 July 1954 (fl & fr), *McCosh* 404 (BM). **Central**: Kali Gandaki, Lete (S. of Tukucha), 3000 m, 9 July 1954 (fl & fr), *Stainton, Sykes & Williams* 1666 (BM); above Maikot, 3300 m, 26 June 1954 (fl), *Stainton, Sykes & Williams* 3262 (BM). **West**: near Tarakot, *c.* 3150 m, 10 July 1952 (fl), *Stainton, Sykes & Williams* 2415 (BM); Tangla Banyang, 3400 m, 17 August 1973 (fl & fr), *Einarsson, Skärby & Watterhall* 3396 (BM).

INDIA (West). Uttar Pradesh: Kumaon, Kalimundi, 2610 m, n.d. (fl & fr), *Strachey & Winterbottom* 3 (BM, GH, K); Tihri-Garhwal, Ganges Valley near Jángla, 2400–2700 m, 10 July 1883 (fl), *Duthie* 976 (BM). **Himachal Pradesh**: Lahul, Manali 3000 m, 2 August 1941 (fl & fr), *Bor* 15587 (K); Simla, Bushahr, Pangi, 8 August 1934 (fl & fr), *Negi Parmanand* 863 (K). **Kashmir**: Bhadawar Distr., Chithar, Kal Nai, 3000 m, 24 July 1943 (fl), *Ludlow & Sherriff* 9228 (BM); Pahlgam, 2250 m, 15 August 1945 (fr), *Stewart* 21696 (K).

PAKISTAN. Hazara: Thandiani, 2400 m, 14 August 1956 (fl & e.fr), *Stewart* 27773 (BM, RAW); Murree Hills, Dunga Gali, 25 August 1962 (fl & fr), *Stewart* 1561 (RAW).

The specimens of *H. himalaicum* proper that most closely resemble the intermediate population from north Myanmar/Arunachal Pradesh, and hence are nearest to 3. *H. trigonum*, are found in central Nepal. From there a westward reduction trend involves merely changes in size, petiole length and complexity. A corresponding eastward trend, however, has resulted in simplification as well as reduction, so that not only do the plants become much smaller in Sikkim, but they become simpler, e.g. the sepals become narrower, acute and entire. Such plants have been confused, by me (Robson, 1977) as well as by Kimura (1966), with the reduced form of *H. wightianum* in south India that, in turn, had been confused earlier (e.g. Dyer, 1874; Keller, 1925; Alston, 1931) with the European *H. humifusum*. The undoubted resemblances between these populations, however, are clearly due to convergence.

The other 'arm' of this eastward trend penetrates into Xizang through the Yadong (= Chambo) gap and continues to north-west Yunnan and north into Sichuan, where it has been known as *H. monanthemum* var. *brachypetalum* Franchet and where the sepals are sometimes entire and rounded.

5. **Hypericum ludlowii** N. Robson in *Notes Roy. Bot. Gard. Edinburgh* **41**: 133 (1983), in Grierson & Long, *Fl. Bhutan* **1**(2): 378 (1984). Type: China, Xizang, Kongbo, Tsangpo Valley, Doshong, 2850 m, 28 July 1938 (fl), *Ludlow, Sherriff & Taylor* 5461 (BM!-holotype).

Fig. 15C, Map 12.

H. monanthemum sensu Li Xiwen in *Fl. Xizangica* **3**: 276 (1986) pro parte quoad t. 114 ff. 3–6.

H. himalaicum sensu Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 57 (1990) pro parte quoad descr. p.p. et t. 12 ff. 1–3.

Icones: Li Xiwen in *Fl. Xizangica* **3**: 276, t.114 ff. 3–6 (1986), in *Fl. R. P. Sinicae* **50**(2): 58, t. 12 ff. 1–3 (1990).

Perennial herb up to 0.4 m tall or long, erect or ascending from creeping and rooting base, with stems slender, growing through other vegetation, unbranched or with short branches from upper or occasionally several nodes. *Stems* 2–4-lined, eglandular; internodes 7–30 mm, exceeding leaves. *Leaves* petiolate, with petiole 0.5–1 mm; lamina 3–20 × 1.5–10 mm, triangular-ovate or elliptic to oblong-oblanceolate, paler beneath, not glaucous, subchartaceous; apex rounded, margin entire, plane, base rounded to rarely cuneate; venation: 3(2) pairs of main laterals from lower third to quarter of midrib, with tertiary reticulation dense; laminar glands pale, punctiform, very small, dense to sparse; intramarginal glands all black or black and pale or reddish, rather dense. *Inflorescence* 1–9-flowered from 1–2 nodes, subcorymbose or broadly pyramidal to cylindric or bifurcate, sometimes with flowering branches from up to 3 nodes below; pedicels 1.5–3 mm; bracts and bracteoles narrowly oblong and black- or red-glandular-ciliate and -auriculate or reduced-foliar and entire without auricles, persistent. *Flowers* (6–)9–11(–15) mm in diam., stellate; buds cylindric-ellipsoid, subacute. *Sepals* 5, subequal or unequal, 1.5–5 × 0.5–1.5 mm, erect in bud and fruit, narrowly oblong or narrowly elliptic to lanceolate, obtuse to acute, glandular-ciliate to entire; veins 5, unbranched; laminar glands linear, all pale or partly black; marginal glands black or reddish, on cilia or sessile or submarginal, sometimes few. *Petals* 5, golden yellow, not tinged red in bud, 4–7 × 1–2.5 mm, (1.3–)1.5 × sepals, oblong-oblanceolate, rounded, margin with black or reddish gland in apiculus and sometimes a few subapical sessile black glands, without or rarely with 1–2 laminar black streaks. *Stamens c.* 20, '3'-fascicled, longest 4–5 mm, *c.* 0.6–1 × petals; anther gland black. *Ovary* 3?-locular, 1.6–2.5 × 1–2 mm, ellipsoid to subglobose; styles 3, 2–2.5 mm, 1–1.4 × ovary; stigmas narrowly to scarcely capitate. *Capsule* 4.5–6 × 2.5–3.5 mm, cylindric-ellipsoid to ellipsoid-subglobose; valves longitudinally vittate. *Seeds* straw-coloured, 0.4 mm, cylindric; testa foveolate-scalariform. 2n = ?

Grassy swamps, streambanks and bogs; 2850–3400(–3600) m.

China (Yunnan, Xizang), Bhutan.

CHINA. Yunnan: Weixi Xian, Pantian Ge, 10 November 1961 (fr), *Kunming Working Stn.* s.n. (KUN). **Xizang**: Tsarung, N. slope of Mt Kenichunpo, May–June, 1932 (fl & fr), *Rock* 22157 (BM, G, K, NY); Nyingchi Xian, Lunang, 3400 m, 4 August 1975 (fl), *Qingzang Exped.* 751280 (KUN, PE); Kongbo, Nayu Chu, 3150 m, 7 July 1938 (fl), *Ludlow, Sherriff & Taylor* 5767 (BM); Mainling Xian, Hongwei Forest Farm, 3200 m, 29 July 1975 (fl), *Qingzang Exped.* 750980 (KUN, PE); Kongbo, Cha, Gyamda Chu, left bank, 2850 m, 31 July 1947 (fl & fr), *Ludlow & Sherriff* 14214 (BM).

BHUTAN. Central: Bhumthang distr., Dhur, 3000 m, 23 July 1949 (fl & fr), *Ludlow, Sherriff & Hicks* 19052 (BM).

H. ludlowii shows a reduction trend westward from Yunnan to Bhutan. The easternmost populations are rather similar to the 'intermediate' population of *H. himalaicum* in northern Myanmar and adjacent India, but differ in the smaller overall size and delicate habit and in the size of the leaves and floral parts, as well as in the absence, in the more reduced forms, of black glands (except in the anthers). The upper leaves in this easternmost population, however, are 'trigonous' as in typical *H. trigonum*. From *H. himalaicum* it differs in the relatively longer styles and narrower acute sepals that are not black-streaked, and it is usually distinct in the smaller flowers, shorter ascending stems and boggy habitat. The styles are not absolutely longer, but the smaller ovary makes them relatively so. It would therefore appear probable, for morphological as well as geographical reasons, that *H. ludlowii* is related directly to *H. trigonum*, not via the *H. himalaicum* 'intermediate' population.

6. **Hypericum daliense** N. Robson, **sp. nov.**
Map 12.

H. wightiano Wall. ex Wight & Arn. affinis, sed foliis maioribus, omnibus sessilibus, elliptico-oblongis integris, floribus maioribus, capsulis cylindrico-ellipsoideis, inter alia differt. Type: China, Yunnan, Tali Range, east flank, 2400–2700 m, July 1906 (l. fl), *Forrest* 4297 (BM!-holotype; K!-isotype).

Perennial herb 0.15–0.4 m tall, erect from creeping and rooting base, with stems single or few, unbranched (always?). *Stems* 4-angled when young, soon terete or faintly 2-lined, eglandular; internodes 2–8 mm, exceeding leaves. *Leaves* sessile; lamina 22–45 × 7–21 mm, elliptic-oblong to (upper) lanceolate, paler beneath, not glaucous, plane, thinly chartaceous; apex rounded, margin entire, base rounded-amplexicaul; venation: 4 pairs of main laterals (lowermost weak) from lower 2/5 of midrib, with tertiary reticulation not prominent, rather dense; laminar glands pale, dense, ± small, punctiform; intramarginal glands dense, black. *Inflorescence* 5–14-flowered, from 1–2 nodes, densely capitate-subcorymbiform; pedicels *c.* 3 mm; bracts and bracteoles lanceolate to narrowly elliptic, with margin and auricles reddish- to black-glandular-ciliate or rarely subentire with a few intramarginal black glands, persistent. *Flowers c.* 10–15 mm in diam., stellate; buds ellipsoid. *Sepals* 5, 4.5–6.5 × 1–1.5 mm, free, subequal or equal, erect in bud and fruit, lanceolate to narrowly oblong-elliptic, acute, glandular-denticulate; veins 5, outer pair branched; laminar glands all pale, linear or usually distal part(s) black, punctiform or striiform; marginal glands reddish or black, on denticles. *Petals* 5, bright yellow, not tinged red in bud, 6–8 × 2.5–3.5 mm, oblong-oblanceolate, margin entire, laminar glands absent, marginal glands few, black, subapical, sessile. *Stamens* 25–35, '3'-fascicled, longest 5–6 mm, *c.* 0.75–0.8 × petals; anther gland black. *Ovary* 3-locular?, *c.* 2 × 1.5 mm, ellipsoid; styles 3, 2–2.5 mm, equalling or slightly longer than ovary, free, divaricate; stigmas narrowly capitate. *Capsule c.* 7 × 4.5 mm, cylindric-ellipsoid, slightly exceeding sepals; valves with dense longitudinal vittae. *Seeds* not seen. 2n = ?

'Open situations amongst scrub in side valleys on the eastern flank of the Tali range' (*Forrest* 4297); 2400–3100 m.

China (north Yunnan).

CHINA. Yunnan: Tali [Dali] range, lat. 25° 40′ N, 2400–2700 m, July 1906 (fl & fr), *Forrest* 4297 (BM, K); Dali, Mt Dian-chang Shan, E. slope of Zong-he-fong, 2500–3100 m, 3 August 1990 (e. fl.), *Murata* et al. 68 (A); Lichiang [Lijiang] Range, March 1933 (fl & fr), *McLaren's Collectors* 176B (BM, K); 'Duplicate of 1912–1913', August 1917 (fl), *Forrest* 15853 (K, W).

H. daliense resembles a large form of *H. wightianum* (to which it is clearly closely related), differing from that species *inter alia* by its larger flowers, larger, all sessile and mostly elliptic-oblong leaves (which are all entire, i.e. the upper ones are not basally glandular-fimbriate) and larger cylindric-ellipsoid capsule. It appears to provide a morphological link between *H. wightianum* and the relatively broad-leaved, few-flowered, south-western form of *H. przewalskii*, and to differ from the other relatives of that form (1. *H. monanthemum* and 3. *H. trigonum* respectively) by the combination of numerous small flowers with glandular-denticulate (not glandular-ciliate to entire) sepals and relatively large elliptic-oblong to elliptic leaves.

7. **Hypericum wightianum** Wall. [*Numer. List*, no. 4818 (1831)] ex Wight & Arn., *Prodr. Fl. Ind. Or.*: 99 (1834); Wight, *Ill. Ind. Bot.* **1**: t. 34 (1838); Gamble, *Fl. Pres. Madras* **1**: 70 (1915); Fyson, *Fl. Nilgiri & Pulney Hill-tops* **1**: 38 (1915), *Fl. S. Indian Hill Stns* **1**: 47 (1932); N. Robson in *J. Jap. Bot.* **52**: 286, ff. 3–4 (1977); Nair & Henry, *Fl. Tamil Nadu*, ser. 1, **1**: 27 (1983); Saldanha, *Fl. Karnataka* **1**: 209 (1984); Robson & Long, *Fl. Bhutan* **1**(2): 377 (1984); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 55,

t. 11 ff. 1–2 (1990); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 78 (1993), in *Fl. West Bengal* **1**: 265 (1997). Type: India, Madras [Tamil Nadu], ex Herb. Wight., n.d. (fr), *Wallich* 4818 (K-W!-lectotype, Robson 1977; K!); Madras [Tamil Nadu], Neelgherries, 1828? (fl & fr), *Wight* 336 (BM!, K!-syntype).
Fig. 13C, Map 14.

H. rubrum Wight ex Dyer in Hook. f., *Fl. Brit. India* **1**: 255 (1874) pro parte quoad spec. cit. excl. typum. Type as for *H. humifusum* L.

H. humifusum sensu Dyer in Hook. f., *Fl. Brit. India* **1**: 255 (1874); Gamble, *Fl. Pres. Madras* **1**: 70 (1915); Alston in Trimen, *Fl. Ceylon* **6**: 19 (1931); pro parte omnes excl. typum.

H. napaulense sensu Dyer in Hook. f., *Fl. Brit. India* **1**:256 (1874) pro parte quoad syn. *H. wightianum* et spec. Maderaspatana; H Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908); Gagnepain in Lecomte, *Fl. Gén. Indo-chine* **1**: 286 (1909); Hand.-Mazz., *Symb. Sin.* **7**: 402 (1931); Rehder in *J. Arnold Arbor.* **18**: 225 (1937); Lauener in *Notes Roy. Bot. Gard. Edinburgh* **27**: 4 (1966).

H. bodinieri H. Léveillé & Vaniot in *Bull. Soc. Agric. Sarthe* **39**: 322 (1904); H. Léveillé in *Bull. Soc. Bot. France* **54**: 594 (1908), *Fl. Kouy-Tchéou*: 198 (1914). Type: China, Yunnan, frontière du Kouy-Tchéou à Kian-ty, bord du fleuve, rive du Yunnan, 9 September 1897 (fl), *Bodinier* 1517 (P? or E?).

H. elodeoides sensu R. Keller in *Bot. Jb.* **33**: 553 (1904).

H. delavayi R. Keller in *Bot. Jb.* **44**: 49 (1909); Anon., *Iconogr. Cormoph. Sin.* **2**: 876, f. 3482 (1972). Type: China, Yunnan, Tschen-Fong-Chan, *Delavay* 5180 (G-BOIS-holotype).

H. monanthemum sensu Pax & Hoffm. in *Repert. Spec. Nov. Regni Veg., Beih.* **12**: 438 (1922).

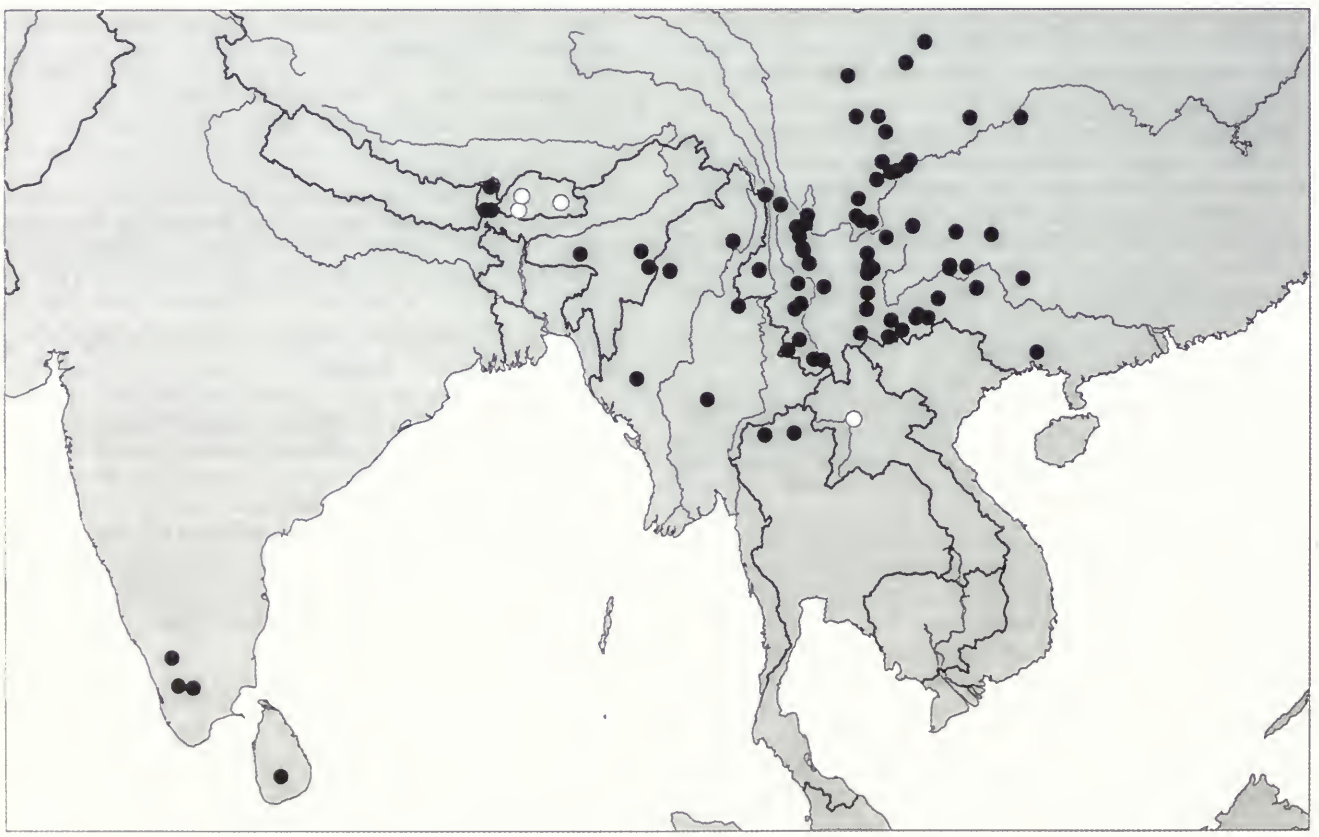
H. nepaulense sensu Craib, *Fl. Siam. Enum.* **1**: 111 (1925).

H. wightianum subsp. *wightianum* sensu N. Robson in *J. Jap. Bot.* **52**: 286, ff. 3.4 (1977); Biswas in Sharma & Sanjappa, *Fl. India* **3**: 80, f. 28 (1993).

H. humifusum subsp. *humifusum* sensu Biswas in Sharma & Sanjappa, *Fl. India* **3**: 67 (1993) pro parte excl. typum et distrib. Europ.

Icones: Wight, *Ill. Ind. Bot.* **1**: t. 34 (1838); Anon., *Iconogr. Cormoph. Sin.* **2**: 876, f. 3482 (1972); Li Xiwen in *Fl. R. P. Sinicae* **50**(2): 56, t. 11 ff. 1–2 (1990).

Perennial or *annual herb* (0.08–)0.13–0.45 m tall, erect to decumbent or procumbent from creeping and rooting base, with stems single or few, clustered, usually branched above but rarely throughout, with branches short, spreading-ascending. *Stems* shallowly 2-lined or terete, eglandular; internodes 9–50(–75) mm, usually longer than leaves. *Leaves* sessile to shortly petiolate (especially lower ones); lamina (6–)10–30 × (3–)5–15(–19) mm, broadly elliptic to obovate or ovate, paler beneath, not glaucous, plane, thinly chartaceous; apex rounded or rarely acute to apiculate-obtuse (Meghalaya), margin entire or (upper) sometimes basally or wholly reddish- to black-glandular-ciliate and with reddish- to black-glandular-ciliate auricles, base rounded to cordate; venation: 2–3 pairs of main laterals from lower third of midrib, with tertiary reticulation scarcely visible beneath, dense; laminar glands pale or rarely a few black, punctiform to striiform, varying in size; intramarginal glands dense or irregular, black. *Inflorescence* 1–*c.* 50-flowered, from 1–2(3) nodes, the whole laxly corymbiform or broadly pyramidal to capitate-cylindric or bifurcated; pedicels 2–3 mm; bracts and bracteoles ovate or lanceolate to linear, with black-glandular-ciliate margin and auricles, persistent. *Flowers* 5–8(–11) mm in diam.,



Map 14 Sect. 9e: 7. *H. wightianum* ●, other records ○.

stellate; buds ellipsoid, subacute. *Sepals* 5, 2.5–5(–6) × 1.5–3 mm, equal, narrowly to broadly oblong or elliptic, acute to obtuse, glandular-ciliate to -laciniate or very rarely entire; veins 3(5), unbranched; laminar glands all pale or some black, linear to punctiform, scattered; marginal glands reddish to black, on cilia, sometimes alternating with intramarginal black gland dots, or very rarely all intramarginal. *Petals* 5, bright yellow, not tinged red in bud, 3–5 × 1.2–1.6 mm, *c.* 1–1.2 × sepals, elliptic-oblong, rounded to acute, margin entire or apically glandular-ciliate, laminar glands absent, marginal glands black, few, distal and subapical, sessile. *Stamens c.* 7–11, '3'-fascicled, longest 2.5–4 mm, *c.* 0.8–0.9 × petals; anther gland black. *Ovary* 1-locular, 1.5– 3 × *c.* 1 mm, ovoid to globose; styles 3, 1.5–2.5 mm, 0.9–1 × ovary, divergent; stigmas narrowly capitate. *Capsule* 3–4.5(–6) × *c.* 3–4 mm, broadly ovoid to subglobose, equalling or slightly exceeding sepals; valves with *c.* 7–9 longitudinal vittae. *Seeds* brown, *c.* 0.5 mm; testa finely scalariform. 2n = ?

Grassy slopes, open woodland, streamsides, marshes, roadsides and rice paddy terraces; 750–3300 m.

South China (Guangxi, Sichuan, Guizhou, Yunnan, Xizang), north Laos, north Thailand, Myanmar (Kachin, Chin, Shan), north-east India (Nagaland, Manipur, Mizoram, Meghalaya, Benghal, Sikkim), Bhutan, south India (Tamil Nadu) and Sri Lanka.

CHINA. Guangxi: Ling Yun Hsien, Loh Hoh Tsuen, 1150 m, 8 June 1933 (fl & fr), *Steward & Cheo* 616 (GH, NY); Lingyun Xian, 7 April 1936 (fl), *Guangxi Prov. Mus.* 11404 (IBSC). **Sichuan**: Huidong Xian, 1750 m, 3 July 1978 (fl & fr), *Zhao Q.S.* 5828 (SZ); Leibo Xian, Shazigou, 1600 m, 27 May 1959 (fl & fr), *Liangshan Wild Econ. Pl. Exped.* 0375 (CDBI). **Guizhou**: Lofou, Pin-fa [Pingfa], April 1906 (fl), *Cavalérie* 2768 (K); Anlong Xian, 1280 m, 26 May 1960 (fl & fr), *Zhang & Chang* 3095 (IBSC). **Yunnan**: East flank of Tali Range, 25° 40′ N, 3000–3300 m, August 1906 (fl), *Forrest* 4298 (BM, K); Anning Xian, Wenquan Gongshe, 1890 m, 4 July 1965 (fr), *Wu C.Y.* 122 (KUN); Pingbian Xian, 1350 m, 20 May 1934 (fl & fr), *Tsai H.T.* 55271 (A). **Xizang**: Gyigang [Zayü] Xian, 2350 m, 30 August 1976 (fl & fr), *Wu* et al. 5266 (KUN).

LAOS. Louang Prabang: Luang-prabang [Louangphrabang], *Thorel* (*fide* Gagnepain, 1909).

THAILAND. Northern: Summit of Doi Angka, 2500 m, 19 August 1927 (fr), *Garrett* 421 (ABD, BM, C, K); Doi Pa Kao, *c.* 1600 m, 8 May 1921 (fl), *Kerr* 5392 (ABD, BK*, BM, K); N. Chiangmai, Doi Inthanon, 2500 m, 30 October 1962 (fr), *Smitanand, Poore & Robbins* 7643 (BK, F).

MYANMAR. Kachin: Irrawadi basin near Tsu-Yo-Ho, 26° N, 1800 m, October 1905 (fr), *Forrest* 829 (BM, K); Kachin Hills, Palaungketaung, 1050 m, 13 April 1912 (fl), *Lace* 5789 (K). **Shan**: Kalaw, 1 May 1931 (fr), *Dickason* 5707(GH); Namkham, May 1933 (fl & fr), *Dickason* 5970 (GH). **Chin**: Mindat, 1350 m, 5 July 1956 (fl & fr), *Kingdon Ward* 2244B (BM).

INDIA. Nagaland: Naga Hills, Kohima, n.d. (fr), *Prain* s.n. (BM). **Manipur**: Ukhrul, 1650 m, 13 March 1948 (fl), *Kingdon Ward* 17083 (A, BM, NY*); Myang Khong, 900–2100 m, February 1882 (fl & fr), *Watt* 6051 (K). **Mizoram**: Lushai Hills, Champnai, 1500 m, July 1926 (fl & fr), *Parry* 63 (K). **Meghalaya**: Khasi Hills, Shillong Peak, 1500–1800 m, 28 July 1949 (fl & fr), *Kingdon Ward* 18677 (A, BM, NY*); Khasi Hills, Barapani, *c.* 900 m, 18–27 April 1954 (fl), *Chand* 754 (L). **Benghal**: Kalimpong, 1200 m, July 1882 (fr), *Gamble* 10471 (K); Darjeeling, Laebong, 1500 m, 22 June 1884 (fr), *Clarke* 35424 (K). **Sikkim**: Rungbee, 1350 m, 5 June 1870 (fl & fr), *Clarke* 11793 (BM). **Tamil Nadu**: Nilgiris Distr., Ootacamund [Udagamandalam], 2100 m, June 1886 (fl & fr), *Gamble* 14348 (K); Palni Hills, Kodaikanal Distr., Madurai, Berijam, 2100 m, 19 November 1985 (fl & fr), *Matthew* RHT 42834 (BM, RHT*); Anamally Hills [Anaimalai], pre-1885 (fl), *Beddome* 388 (BM).

SRI LANKA. Central: Nuwara Eliya Distr., Pattipola 1980 m, 21 June 1972 (fl & fr), *Hepper* 4441 (K).

BHUTAN. South: Chukka Distr., Chukka and Marichong. **Central**: Thimpu Distr., Thimpu Chu Valley; Mongar Distr., Sengor. All *fide Fl. Bhutan*: 378.

H. wightianum is clearly closely related to *7. H. daliense* and has apparently spread from south-east China westward to Sikkim and south-westward to western Myanmar and Mizoram in India. It then reappears in the south Indian hills and in Sri Lanka. Morphological variation follows these trends:

(1) The erect to basally decumbent form extends along the Himalaya and also occurs in Meghalaya, Myanmar and the Nilgiri Hills. It has sessile leaves, the upper ones having near-basal glandular cilia and glandular auricles.
(2) In Thailand form (1) gives rise to a decumbent form with slender stems and shortly petiolate leaves, the inflorescence being a small version of that of form (1).
(3) A form similar to (2) occurs in south India (Kodaikanal), except that the leaves vary from sessile to petiolate. This gives rise to a form in the Anaimallai and Nilgiri Hills with petiolate entire leaves and entire sepals and bracts (e.g. *Beddome* 388) (*'H. rubrum'* or *'H. humifusum'* of Indian Floras). One of these Anaimallai specimens (*Beddome* 386) has sessile leaves.

All these variations are continuous. The form that is most similar to 6. *H daliense* occurs in Khasiya (Meghalaya).

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SYSTEMATIC INDEX

Accepted names are in roman and synonyms in *italics*; new names and principal references are in **bold**. An asterisk denotes a figure. A = sect. Ascyreia, B = sect. Bupleuroides, C = sect. Concinna, E = sect. Elodeoida, M = sect. Monanthema, R = sect. Roscyna, S = sect. Sampsonia.

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A bibliography of the scientific work of Boris V. Skvortzov (1896–1980) with commentary on the publications concerning diatoms (Bacillariophyta)

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CONTENTS

SYNOPSIS. This paper presents a full bibliography for the naturalist Boris V. Skvortzov. Special attention has been given to his diatom (Bacillariophyta) studies. Skvortzov was fortunate to have had access to material from many areas which had never been studied for their diatom flora. In this paper we present a detailed list of those localities.

INTRODUCTION

The scientific career of Boris Skvortzov [Skvortsow, Skvortsov] (1896–1980) spanned nearly 70 years: he published his first paper in 1916 when just 20 years old and his last papers appeared posthumously between 1981 and 1985. As far as we have been able to establish, during that period Skvortzov published some 434 papers, notes and popular botanical accounts mostly relating to the area of Manchuria in north-east China. Skvortzov was predominantly interested in microalgae, particularly diatoms, but published a great deal in many other botanical areas.

Contemporary reaction to Skvortzov's work, at least from the perspective of phycologists, is somewhat mixed. Skvortzov did indeed have a penchant for naming many new taxa – indeed most of his floristic diatom accounts are predominantly descriptions of new taxa. Yet this in itself is not the largest obstacle to understanding and coming to some informed judgement of Skvortzov's work. He was able to examine material from parts of the world that had hardly, if ever, been studied before, but practically none of his material is available for study today, and very little has found its way into existing herbaria. Why not, then, simply consign his work to history, regard his new taxa as unverifiable and rely on current accounts made from the same areas? We believe that this option seems a little premature, although it is worth noting that some researchers studying flagellates have opted for that approach (Patterson, 1994: table 5). We have developed a slightly different view and this contribution is a preliminary start on gaining an understanding of Skvortzov's work and will ultimately contribute to a greater understanding of diatom diversity in north-east China.

Our specific interest in Skvortzov developed from recent studies on Lake Baikal, Siberia under the auspices of a 'Darwin Initiative for the Survival of Species' study (Flower & Williams, 1999). The Darwin Initiative (DI) allowed us to make a systematic collection of diatom samples from the entire lake at regular intervals and regular depths. In addition, we had the opportunity to revisit and re-sample the localities Skvortzov examined. Skvortzov was not the first to write about and describe the many diatoms of Lake Baikal, but he was the first to recognize and identify many of its taxa as endemic. His diligence, with the deep water Lake Baikal sample at least, can

be appreciated by his comment that 'I have examined about a hundred microscopic slides from this place...', (Skvortzov, 1937:297). It would be surprising if anyone working today dealt with such large numbers of preparations from a single site. (Skvortzov (1936: 9) notes the same approach for his study of Kizaki Lake in Japan: 'I have examined a hundred microscopic slides...Half a year was spent in the study of this collection'.)

Our own studies suggest that far from being rather optimistic concerning the diversity of Lake Baikal diatoms, Skvortzov may have under-estimated Lake Baikal's benthic diatom diversity (see Mann, 1999). If Skvortzov was reasonably accurate in this study, there seems no reason to doubt his work elsewhere – or at least until such time as relevant material becomes available and can be examined.

A second aspect that we felt required attention was that as Skvortzov had written some of the first accounts of north-east Chinese diatoms, and we were struggling to understand the biogeographic relations of the area relative to our Lake Biakal samples, a survey of the areas he did study was of significance. Considerably more attention is now being paid to the idea of regional diversity of diatoms and to their significance in biogeographic studies (Kociolek & Spaulding, 1999).

Bearing these ideas in mind, in this paper we have tried to achieve three things that may act as a baseline for further examination and evaluation of Skvortzov's diatom studies. It is of some significance that Chin (1951:151) wrote: 'During the past hundred years Skvortzow was the most ardent worker.'

(1) The biggest outstanding problem when dealing with Skvortzov's work is that very little of his original material is available. To address this issue, we have compiled a list of the material Skvortzov examined. A good deal of this material was given to him by other collectors and the possibility remains that some still exists in various herbaria around the world. We have been able to trace some original material in the diatom collections at the BM and are aware that other sub-samples exist in the California Academy of Science, Bremerhaven in Germany, and the Department of Paleobotany, Swedish Museum of Natural History. A list of geographical areas may allow new or recently collected material to act as neotypes should Skvortzov taxon names be confirmed. We have begun this process by designating neotypes from the DI material for some Lake Baikal diatoms we have examined in detail (Reid & Williams, submitted).

(2) We have compiled a bibliography of all his writings as far as we have been able to establish. A number of the entries have not been seen by us but have been taken from bibliographies Skvortzov published himself. Tracing Skvortzov's published work is a complex business simply because many of the places he chose to publish at that time were small local natural history societies whose existence was sometimes rather short, exacerbated by the volatile nature of Manchuria during the years he was living and working there. Fortunately for us, many of these publications are held in the various libraries of The Natural History Museum, London (BM). We have numbered all the items in the bibliographic section and refer to these numbers in the remaining text. For instance, Skvortzov's three bibliographies can be found under items 300, 396 and 418. References to work not written by Skvortzov appear at the end of the paper and are referenced in the usual way. With respect to Skvortzov's publications, two articles have been published that review his contributions. Unfortunately, we have been unable to trace copies of either (Uedo, 1940; Baranov, 1959).

(3) As our area of interest is diatoms, we have marked those publications which mention or list diatom species, new or otherwise. We have resisted the temptation to list all of Skvortzov's taxonomic names at this stage, simply because the large amount of Chinese literature needs to be taken into account and it would serve no immediate purpose other than to highlight various permutations of names.

A SHORT BIOGRAPHY

Although Skvortzov lived most of his life in Harbin, north-east China (he was born in Warsaw in 1896, moving to Harbin in 1902), he travelled to St. Petersburg during the years 1914 to 1917 to train as a diatomist under R.W. Kolbe (Selling, 1962) and S. Wislouch. With the exception of some time spent collecting material and learning English in Fuzhou, Fujien, China (1918–1919),[1] Skvortzov remained in Harbin until 1962 when he departed for Brazil where he spent his remaining years.

During his time at Harbin, he was actively involved in the Manchurian Research Society and was in charge of their cryptogamic plants (*Review of the Manchurian Research Society*, 1926:13). On his return to Harbin from Fuzhou, Skvortzov noted that from 1919 to 1935 he taught botany. He was heavily involved with the Manchurian Research Society, acting as their secretary, which he probably undertook on a voluntary basis: 'the shortage of funds did not permit to engage a special personnel for the station, and all work was carried on voluntarily by a few members of the Manchuria Research Society in their leasure [*sic*] hours' (Pavlov, 1925:9). From 1923 to 1928, the period covered by written reports, Skvortzov gave numerous presentations, especially to the 'Young Archaeologists, Naturalists and Ethnographers Association of Harbin' (he gave two presentations in 1923, six in 1924 and seven in 1925). Skvortzov published most of his diatom studies between 1919 and 1939. After that time, and especially while living in Brazil, he worked and published mainly on flagellates. We have no expertise with those organisms and leave any evaluation of that work to those who do.

We were unaware of any existing portraits until recently when we discovered a number in the various publications of the Manchuria Research Society. The reports of the society include a number of group photographs that include Skvortzov. In the *Review of the Manchurian Research Society* (1926, tables 2 and 3), Skvortzov appears in a group photograph of the 'Members of the M.R.S. committee presided over by Doctor Wang Tsin-Tschung. (1924)' and a group photograph of 'Members of the M.R.S. committee presided over by Doctor Hei-Show-Djen (1925)'. Other photographs include Skvortzov with 'The American explorer prof. [*sic*] Hansen, seated amid the members of the Natural History section attached to the M.R.S.' (Fig. 2) and a portrait of Skvortzov partially hidden by a giant water lily (Figs 1 & 3).

In a later report, there are group photographs of the Manchurian Research Society that includes Skvortzov; 'Vice-president of the Chinese Eastern Railway Board of Directors Mr. Lashevich surrounded by members of the Manchuria Research Society Committee after having viewed the Museum' and 'Manchuria Research Society Members of the Committee and Revisional Committee, elected in 1927' (*Review of the Manchurian Research Society*, 1928: tables 2 and 6).

[1]The *Journal of the North China Branch of the Royal Asiatic Society* (50:259) listed Skvortzov as a member, giving his address as 'c/o C.M. customs, Foochow'.

Fig. 1 Skvortzov holding a giant water lily. From the *Review of the Manchurian Research Society* (1926).
Fig. 2 Boris V. Skvortzov. From the *Review of the Manchurian Research Society* (1926).

Fig. 3 Skvortzov partially hidden by a giant water lily. From the *Review of the Manchurian Research Society* (1928).

A further photograph is included in *Naturalist Man'chshurii (Naturalist of Manchuria)* (1936:64). The caption reads 'Anniversary day of association A.N.E. – July 26 1936. The members of the association and their friends.'

A SUMMARY OF THE DIATOM MATERIAL SKVORTZOV STUDIED

The majority of Skvortzov's material came from the area known as Manchuria which has been largely understood as north-east China. Manchuria can be separated from the Russian Federation largely by the Amur, Argun, and Ussuri rivers, from North Korea by the Yalu and Tumen rivers, and from Mongolia by the Da Hinggan (Great Khingan) Mountains. Manchuria also includes the Liaodong peninsula. Provincial divisions have changed frequently and since 1956 Manchuria has comprised Jilin, Heilongjiang, and Liaoning. Much of the region is mountainous. The Da and Xiao Hinggan (Great and Lesser Khingan) in the north and the Changbai in the east are the greatest ranges. Material has been grouped to largely correspond to modern geographical areas.

Each entry below is identified by the relevant published reports and a collecting date if given. Future work will concentrate on the new taxa Skvortzov named and the possible material that can be, or has been, used for typification.

China

Fujian (Fukien)

FUZHOU (FOOCHOW, MINHOW). Skvortzov studied several collections from Fuzhou most of which he collected himself in 1918 and 1919 (item 418:389); Chung (1929:125) gives a brief account of Skvortzov's visit.

1917 (item 61): The first article was based on material collected by Mrs W.R. Myers 'in the environs of Foochow…the material was examined in the Petrograd Academy of Science in 1917' (item 61:205). Skvortzov examined the material in the Petrograd Academy suggesting that this study may have been under the supervision of Kolbe and Wislouch, leaving open the possibility that this material may still be in St. Petersburg (Petrograd).

1918 (item 139): This was the first account of material collected by Skvortzov during his trip to China: 'Being in Foochow in 1918 some observations were made by me during the winter time on the life of the plankton of the fishponds' (item 139:190).

1918 (item 259): Material collected by Skvortzov 'on the seashore of Fukien Province, near Foochow, China, during the winter of 1918' (item 259:151).

1918 (item 427): This material is presumably part of the collection made by Skvortzov in 1918. One collection was noted as the type material for *Porosularia meisteri* Skvortzov and *Porosularia merrilli* Skvortzov, ('Hab. in Stagno prope oppidum Foochow, prov. Fukien, China australis, lg. B. Skvortzov, in 1918', item 427:413) and another for the type material of *Porosularia borgei* Skvortzov ('Hab. in orizetis prope oppidum Foochow, prov. Fukien, China australis, lg. B. Skvortzov, 1918', item 427:415).

February 1919 (item 140): Material collected by 'Mr. C.R. Kellogg, . . . at the end of February 1919 in Kokchiang, 70 miles from Foochow...' (item 140:195).

No date (item 427): Some additional samples were included in this report, the collections probably also dating to 1918: 'River Ming, in the environs of Foochow City, prov. Fukien, South China' (type of *Pinnularia kisselewii* var. *subacuta* Skvortzov) (item 427:400) and '...swamps of Foochow, prov. Fukien, South China' (type material for *Pinnularia meyerii* var. *hinganica* Skvortzov) (item 427:400).

XIAMEN (AMOY)

1924 (items 222, 386, see also **item 194 & 427)**: Material collected by Dr H.H. Chung in the winter of 1924. More details of the locality were given in a later paper by Skvortzov: '...Hab. In stagnis prope oppidum Amoy, prov. Fukien, China australis, Leg. H.H. Chung, a. 1924' (item 386:378, item 427: 412 & 414). This material served as the type for *Porosularia amoyensis* Skvortzov and *Porosularia kolbei* Skvortzov (item 427:412 & 414).

TIANJIN (TIENTSIN). Collections made by Skvortov in early 1919 were used for two studies (detailed below). His general botanical work from this period is covered in a series of papers entitled 'Notes on the agriculture botany and zoology of China' (items 59–90, 105–110, 125–132, 138–140).

17 March 1919 (item 138, 190): 'Being in Tientsin in March 17, 1919 a small collection of Algae was gathered by me in the ponds of the Russian Garden and near brick-kilns' (item 138:189; item 190:102).

KULIANG RIVER

1918 (item 228): Material collected by Skvortzov 'at Kuliang, Fukien Province, in South China. This place is 9 kilometers from Foochow, and is 2,400 feet above sea level' (item 228:39).

Jiangsu (Kiangsu)

SUZHOU (SOOCHOW). Several samples from Suzhou were noted by Skvortzov in item 330, collected by Dr H.L. Li in 1934. Skvortzov later (item 402) gave descriptions of the same taxa, noting the troubled publication history of this study: '...this manuscript was published by the author in Proceedings of the Harbin Nat. Hist Sc. in 1946...' (item 402:59). The 1946 paper (item 330) therefore still has priority in spite of it being hard to obtain.

1934 (item 330 & 402): 'China media prope Soochow prov. Kianghsi Dr. H.L. Li, 9/8 34'. Skvortzov described several new taxa from this locality. One locality is given with the date '9/9, 34'. We suspect that the month of collecting in erroneous in one or other of the reports as Skvortzov later states that the new taxa were based on one sample provided by Dr L. Li 'in the lake in the City of Soochow of prov. Kiansu...in 1934' (item 402:59).

POYANG

October 1929 (item 287): Material from Rev. Umberto Verdini, 'from the Eastern Lake of the city of Poyang, Hunan, China, on lotus leaves' (item 287:465). While the title refers to Hunan, Chin (1951:156) points out that Poyang Lake is in the northern part of Kiangsu and not in Hunan. The material is referred to again in item 405.

Zhejiang (Chekiang)

HANGZHOU (HANGCHOW)

12 August 1933 (item 297): Material collected from '...a sample of mosses...' by Mr I. Kovalchook-Koval 'in a cave on a rock in the environs of Hangchow...' (item 297:219). Kovalchook-Koval made a number of collections and contributed to the many *Manchurian Research Society* publications.

Liaoning

DALIAN (DAIREN)

1926 (item 226): Material from 'my young friend A. Prosowetsky a small collection of sea mud, from oysters collected at Dairen' (item 226:419).

Shandong (Shantung)

SHANWANG – MIOCENE FOSSIL

1935 (item 308, 330): Skvortzov reported that this material was 'sent to me some time ago by Drs. C.C. Young and P. Teilhard de Chardin of the Geological Survey of China' (item 308:193). He described the material thus: 'diatomaceous earth forms a thick formation at Shanwang near the city of Linchü, eastern Shantung, about half way between Tsinan and Tsingtao, not far south from the railway' (item 308:193). According to Skvortzov, this was the first Chinese freshwater diatom fossil deposit. In an earlier report, Young (1936) provides more details of the deposit and when it was collected ('A closer examination of the region was evidently necessary, and I carried it out in May 1935', Young, 1936:172). Young adds in a footnote: 'The papyrus shales are a diatomaceous earth, the botanical study of which has been undertaken by Dr. B. Skvortzov. Most abundant are the frustules of *Melosira granulata* (Her.) Ralfs. A paper by Dr. Skvortzov will be published in the Bulletin' (Young, 1936:175, footnote 1). As for the age of the material, 'After careful examination, Hu believes that the age of the flora is probably Miocene...' (Young, 1936:177) and '...we have to consider the Shanwang series as Upper Miocene in age' (Young, 1937:280).

Material we believe to be from the same source was also studied by Voigt (1937). He says of this material, '...a certain quantity was kindly placed at the disposal of the writer by Dr. W.H. Wong of the National Geological Survey of China...' (Voigt, 1937:311). Voigt also states that 'So far only one authentic deposit of diatomeaceous earth has been reported in China, namely, that from Shan-wang in the Lin-chu district of Shantung, which was discovered by Dr. C.C. Young of Peiping' (Voigt, 1937:311). Some of Voigt's material is housed in the BM and some preliminary electron micrographs have been published (see Williams et al., 1998:59, figure 2–5, electron micrographs of *Tetracyclus emarginatus* var. cf. *parvula* Forti, see also p. 55, footnote 8; BM s.n.). Further examples of this material are housed in the Palaeontological Museum of Stockholm.

Item 330 contains repeat descriptions of two taxa first described as new in item 308.

Sichuan (Szechwan)

CHENGDU (CH'ENG-TU)

March 1926 (item 317): '...two tubes of diatom material from the environs of that city [Ch'eng-tu], collected in March, 1926' (item 317:479). The material was donated by Dr H.D. Brown of West China Union University, Chengdu, Sichuan. Some further commentary and notes are in item 405.

Heilongjiang (Heilungkiang, Heilungtsiang)

VARIOUS LOCALITIES

1950 (item 426): 'Amur prope Oopu', part of A.I. Baranov collecting trips (type material for *Pinnularia zabelini* var. *amurensis* Skvortzov).

1951 (item 427): Material collected by Skvortzov, 'Hab. In lacu alkalini prope Stationem Sun, prov. Heilungtsiang, Manchuria borealis, China, Skvortzov, 15.9.1951' and used as the type material for *Porosularia poroidea* Skvortzov and *Porosularia subsalsa* Skvortzov.

No date (item 405): 'In regionis montanis, Prov. Heilungtsiang, Manchuria borealis, China'.

HARBIN

1915–1917 (item 160, 171): Skvortzov lists six samples in item 160 and eight samples in item 171. The samples were collected by various people including Skvortzov: B.R. Arnold, S.W. Schernich, M.A. Hintze, N.A. Schemilewitch and M.G. Dorian. Of these collections, the information given is, in most some cases, of little significance in establishing exact locations and dates of collecting. For instance Skvortzov's own collecting is given as '...from the environs of Harbin collected by me...' (our translation) between 1915 and 1917. The most precise dates and details are given for B.P. Arnold (during August 1916), N.A. Schemilewitch (July 1916) and M.G. Dorian (August 1916).

1927 (item 312): Material collected by Skvortzov. Three samples were examined: (1) from Harbin, 20 September 1927, 'from the bark of *Ulmus manshurica* Nakai'; (2) from Eastern Harbin, near Maoershan Railway Station, 20 July 1927, 'on mosses on rocks along a mountain river'; (3) from Eastern Maoershan, near Mifun Station, 5 September 1927, 'in mosses on mountain rocks' (item 312:263).

No date (item 66): Material described simply as 'The algae just described were studied from numerous collections gathered near the railway line in North and Middle Manchuria and mostly in the environs of Harbin...' (item 66:63).

SONGHUA (SUNGARI) RIVER, HARBIN

17 March 1923 (item 211): Material collected from the Sungari River for a study on winter phytoplankton. The report lists ten species of diatom.

28 August 1935 (item 305): 'The material was collected 28 August 1935 by one of my enthusiastic collectors Mr. I. Kovalchook-Koval on a shore of a swampy lake on the Sungari river plain, three miles from the Sungari railway bridge' (item 305:783, including a photograph of the site, fig. a). A short account of the expedition is given in Anon. (1936).

August 1936 (items 302–304): Plankton samples collected on the 9 August 1936 by Mr N.I. Nikitin, from a 'marshy branch[es], along sand-dunes' of the Sungari River (item 302:628). The diatoms are listed in part II of a three part study of this area (item 303). Skvortzov used the material for further taxonomic revisions in a later study (item 330): 'Hab. Manshuria bor., prope Cheng st. in stagna fl. Ashiho, M. Nikitin, 10/8 1936'.

Beijing Municipality

BEIJING (PEKING)

March 1926 (item 219): Collections made by Prof. N.G. Gee and Dr H.J. Chu 'in the environs of Peking' (item 219:43). In all, three lakes were sampled. Previously, Gee published a list of diatoms from Suzhou and Ningbo (Gee, 1926). A name change is given in item 330:26 (*Nitzschia regula* f. *pekinensis* Skvortzov is replaced with *N. regula* var. *robusta* Skvortzov).

Shanghai

June 1918 (item 70): Material collected by Skvortzov from a pond near the Public Gardens in Shanghai (item 70:66).

19 May 1933 (item 310): Material collected by Mr I. Kovalchuk-Koval 'a sample of mosses collected by him on the bark of a tree in Shanghai...' (item 310:443).

Hongkong

August 1957 (item 420): Collected by Mrs V.T. Mamchyi 'from mosses grown on the trunks of a tree in Hong-kong, eastern Asia' (item 420:407).

Inner Mongolia

HINGGAN LING (KHINGAN MOUNTAINS)

1922 (item 213 and 330): Collections made by Skvortzov from the 'Khingan Mountains in the environs of the Fuleierdi Railway Station' (item 213:39). Further details given in item 330: 'Hab. Manshuria bor., in rivulos fl. Jal prope Barim, Khingan montibus'.

1951 (item 426 & 427): Material from the 'Northern part of Great Khingan Mountains from the western corner of Inner Mongolia, China. Collected during a botanical expedition made in August of 1951 by the Botanical Section of the N.E. China Agricultural Institute of Harbin' (item 426:111). The material is composed of two samples of moss extracts (details are given in item 426:119). The samples were collected by Skvortzov who gives a full description of the collecting trip (item 426:112). The paper makes reference to an unpublished manuscript (*Bacillariophyta in Illustrated flora of North-Eastern China,* 1957, 'deposited in Herbarium of Forest Academy in Harbin, China') which contained the first descriptions of the new taxa subsequently validated in this report.

ARGUN RIVER, DALAI-NOR

August 1926 (item 227): Twelve tubes of material collected by Mr. P.A. Pavlov '...in the northern part of Dalai-nor Lake in August, 1926'. (item 227:31).

1927 (item 314): Material collected by Mr P.A. Pavlov during the summer of 1927 'in the environs of the Chalainor station of the Chinese Eastern Railway, at the source of Argun River, which arises from Dalai-nor or Talaihu Lake' (item 314:43).

1950 (item 427): 'River Argun, A.I. Baranov, 1950' as type material for *Cymbella lanceolata* var. *grossepunctata* Skvortzov.

VARIOUS COLLECTIONS

1916, 1918, 1928, 1931 (item 289): This paper is divided into four parts. The first part deals with collections made from Bagah Oulan on the 18 September 1918 on Licent's travels to Kansou and Kou kou noor. Some further details of the expedition are given in Licent (1936:5 & 11). The second part deals with collections made from Yen tchê in the province of Chansi in 1916, 'Chensi Central: vallée du Wei ho, les Alpes chinoises' (Licent, 1936:5). The third part deals with collections made in the environs of Kalgan, near a lake. No specific details are given in item 289 but the material may have been collected during the expedition described by Licent (1936:7), of a visit in 1931 to the Mongolian Interior, Kalgan. The fourth part deals with collections made in the North of Manchuria, in the province of Kirine, to the west of Harbin, on July 1928 (item 289:36; Licent, 1936:7).

RIVER IMINGOL

1925 (item 209): Material collected by J.W. Tokmakoff 'in freundlichster und dankenswertester Weise Bacillariaceen-Material aus dem Fluss Imen-gol, 80 Kilometer von Hailar' (item 209:311).

Some further are details given in item 330: 'Mongolia occidentalis, fl. Imingol prope Hailar, J.V. Tokmakov, 1925'.

Tibet

1901 (item 69): Material collected by Mr. Ladigin 'during the expedition in Tibet in 1901...' The collections mentioned were from three lakes: (1) 'plankton...freshwater lake Kurlyk-nor [1 June 1901] in the Tsaidam district...' (2) '...salt lake Toso-nor [3 July 1901]... not far from lake Kukunor...' The samples were '...examined in the Petrograd Academy of Science' (item 69:66). The list of species (containing only two diatoms) was from (3) Khara-nor.

Russian Federation

Jakoutsk

1912 (item 3): Material collected by Mr G. Dolenko '...pendant une expedition, organisée par le Comite de migration' (item 3:19). No further details have been discovered.

Primorsk

Lake Tshla

5 August 1916 (item 5): Material collected by Lake Tshla 'se trouve prés de l'embrouchure de l'Amour et de la ville de Nikolaievsk' (item 5:20) ['close to the mouth of River Amur and the town of Nikolaievsk'].

Khanka (Hanka) Lake, near Vladivostok

1924 (5, 16, & 24 July; 4, 11, 15, 20 & 23 September; 15 August) (item 234): Material collected by E.N. Klobukova-Alisova in 1925 and by E.N. Klobukova-Alisova and A.G. Hahina in 1924 during the South Khanka Botanical Expedition made by the Southern branch of the Geographical Society of Nikolsk-Ussurisk. Seventeen samples are listed with collection numbers. Some further notes are made in item 330.

Vladivostok

1928 (item 258): Material collected by Skvortzov during the summer from 'Golden Horn Bay and from Cape Basargino near the Pacific Fishery Research Station' (item 259:129) on a visit to Vladivostok.

No date (item 220): Material collected from Vladivostok '...from sea-weed *Laminaria* sp.' (item 220:57).

No date (item 315): Material received from Mr I.P.Popov, 'a sample of diatoms collected by him during a botanical survey of Primorsk Province in a *Carex-Sphagnum* peaty bog in Lianchiho River Valley, about 40 kilometres east of Vladivostok, not far from the seashore' (item 315:161).

Amursk

Khabarovsok (Habarovsk)

1909–1916 (item 40, 43, 66 & 254): Samples collected from the River Amur 'pendant les expeditions de 1909 á 1916, en Extreme Orient, entreprises par le Department d'Agriculture' (item 40:21). In two later reports, Skvortzov adds that the samples were collected by W.K. Soldatow 'during the expedition of the Department of Agriculture in 1910 to 1914...largely plankton obtained from the Amur river, near Habarosvk' (item 254:69) and 'also from collections of the Amur river made by W.K. Soldatow...' (item 66:63).

River Amur

1928 (item 311): Material collected by Skvortzov during the summer 'in the environs of Okeanskaia station, near Amur Bay, in a forest Hypnum bog' (item 311:251).

1951 (item 386): Skvortzov described several new taxa from Amur River material: 'Hab. In fl. Amour, Siberia, Leg. A.I. Baranov a. 1951' [item 386:375].

River Zeya (Zeja)

1909–1910 (item 6): Material collected by Mr J. Abramov 'du fleuve Zeja (province Amourienne)...dans les environs de la station meterologique de Bomnak...' (item 6:128).

1950 (item 427): Material described by Baranov, 'fl. Zea. Districtus Amurensis, Siberia orientalis, lg. A.Baranov, 1950' and used by Skvortzov to described new taxa from Amur River' (type of *Pinnularia zabelini* Skvortzov and var. *zeaana* Skvortzov, item 427:414 type of *Porosularia pseudoviridis* Skvortzov).

Siberia

Lake Baikal

1916, 1925–1926 (item 210): The material came from several expeditions made by C.I. Meyer. Skvortzov listed 36 samples, nine from 1916, 11 from 1925 and 16 from 1926. Meyer (1930) presented his own detailed account of the algae from the samples he collected during these expeditions, as well as presenting his accounts of the samples Skvortzov studied. Meyer's descriptions of the samples are somewhat more detailed than Skvortzov's account.

There has been some debate as to whom was actually responsible for the new taxon names in the 1928 publication (item 210). Much later Skabichevskij (1974) established that Skvortzov alone was responsible, as Meyer (1930) presented his own account a few years later in which not only did he differ from Skvortzov in a number of places but also he noted that he was solely responsible for collecting the material (Meyer, 1930:327). A similar statement was made in Skvortzov and Meyer: 'Since 1926 B.W. Skvortzov has joined prof. [*sic*] C.I. Meyer to work together on the identification and classification of the Diatoms *collected by the latter* in the Baikal lake and this work is but a preliminary report of the work' (item 210:2, italics added). Hence it seems justified to consider the taxonomic work as Skvortzov's alone. The correct attribution for the new taxa in item 210 should therefore be 'Skvortzov in Skvortzov & Meyer' (see also Kociolek & Stoermer 1988:96–97).

29 July 1916 (item 307): Nearly ten years after the first paper on Lake Baikal, Skvortzov re-examined in detail one sample at '33 meters near the Ohlon Gate of Baikal Lake...' (item 307:297). This sample is also listed in Skvortzov & Meyer (item 210:2; '7. 29/VII 'Olhinskie vorota'. Haringari bay, at a depth of 33 metres').

A number of taxonomic changes are made in item 330.

Some of Meyer's Lake Baikal material is available in the California Academy of Science and Bremerhaven (Kociolek & Stoermer 1988:95–96). New collections from Lake Baikal (housed at BM), made as part of the DI (Flower & Williams, 1999), will be ideal for designating neotypes as many of Meyer's collecting sites were revisited and are subsequently being re-studied (Reid & Williams, submitted).

No date (item 426 & 427): Some additional material from Lake Baikal was noted in this later report: 'River Kitschera near Lake Baikal, Siberia' (type of *Pinnularia kisselewi* var. *attenuata* Skvortzov), 'Lake Baikal' (type of *Pinnularia dorogostaiskii* var. *latior* Skvortzov) (both in item 427) and 'River Selenga prope Baikal, Siberia' (type of *Pinnularia lata* var. *intermedia* Skvortzov) (item 426).

KENON LAKE, TRANSBAIKALIA
No date (item 313): Material collected by Miss K.V. Okunozova, '...near the shore of the lake, from twigs and leaves of *Potamogeton* sp.' (item 313:399).

RIVER KHOLOY (CHOLOY)
No date (item 43): Material obtained from 'l'Amour par l'expedition de Mr. Korotky ...dans le fleuve Choloy en Transbaikalie par l'expedition de Mr. Korotky...'. (item 43:22).

Tyva

RIVER YENISSEI
1925–1926 (item 386, 403): Material collected by P.J. Usachow and described as '...Hab. In fl. Ienissei prope oppidum Krasnojarsk, Siberia, Leg. P.J. Usachow, 1925–1926' (item 386:376). Many years after receiving the material Skvortzov noted: 'The author received the diatom samples from Yenisei River in 1927 while he was working in Harbin, China from the Hydrobiological station of Krasnojarsk City, Siberia. A series of slides was prepared by the author from these collections and preliminary studies made in 1930–1931' (item 403:57). The material was used for some taxon descriptions in item 399, which provides more precise dates. The collections include material for *Pinnularia viridis* var. *tubensis* Skvortzov, *P. viridis* var. *minuta* Skvortzov, ('Ienissei prope oppidum Krasnojarsk, Col. 17, 11. '26') and *P. viridis* var. *tumida* Skvortzov ('In fl. Jenisei, Siberia media, lg. 26.6. '26'.)

The Altai Mountains

The Altai Mountains in southern Siberia form the major mountain range in the western Siberia region and provides the sources of the rivers Ob and Irtysh. The main areas of the region are Altaysky, Zapovednik and an area surrounding Teletskoye Lake. The entire area is enormous and Skvortzov's samples are limited especially as most of his reports lack useful details.

1897 (item 41): Material collected by Mr Silantiev 'dans les sources "Rachmanovsky" de l'Altai.' (item 41:21).

Kaolingtze

15 July 1926 (item 316): Material collected by Skvortzov, on 15 July 1926 'in the mountain ranges near Kaolingtze station of the Chinese Eastern Railway, about 300 miles east from Harbin, I collected a sample of diatoms from a little mountain bog of forest mosses' (item 316:343). The material was probably used in item 427 as the type material for *Pinnularia fritschiana* Skvortzov.

Kazakhstan

Akmolinsk

KURGAL'DZIN LAKE. These early collections were probably studied in St. Petersburg and may have been retained in that institute.

June 1899 (item 42): Samples of *Chaetoceras wighamii* Brightwell from 'le bassin du lac Kourgaldjin de la province d'Amolinsk.' As noted in item 252, 'The presence in the Kokai Lake and Nura River of *Chaetoceras Wighamii* Brightwell...is interesting' (item 42:33). The collecting date for Nura River is given as 8 June 1899 and for Kokai Lake is given as 23 June 1899.

June 1912 (item 7): Collected by Mr Ganeshinn (Ganesin) 'provenant du lac Courgaldgin' (item 7:128).

VARIOUS LAKES INCLUDING TELETSKOI (TELETSKOE) AND KURGAL'DZIN
1899, 1901 (item 252, 246): Material provided by Prof. G.I. Vereshagin, collected by P.T. Ignatow 'in lakes of the Akmolinsk district of Siberia in 1899 and 1901' (item 252:33). There were 20 samples, all listed. Item 246 is a short report on a sample from Lake Teletskoi taken in 1901 by Ignatow.

BLACKHACH (BALKACHE) LAKE
No date (item 42): Material collected from 'le lac salin d Ala-Koul, situe dans le partie ouest du lac Balkache' (item 42:22).

ZAYSAN (ZAISAN) LAKE
1905 (items 193, 203): Material collected by A.N. Sedelnikoff (Sedelnikov) 'in lakes in the Altai Mountains of South Siberia. All the samples were gathered in the environs of Zaisan Lake...' (item 193:249). Further comments on the material can be found in item 203. There is some overlap of material studied in these accounts but they are largely complementary suggesting they are all from the same source. Skvortzov refers to a detailed account of Zaysan Lake written by Sedelnikoff (1905), a book we have been unable to trace.

MARKAKOL' (MARKA-KUL) LAKE
8 July 1912 (item 8): Material collected by Mr A.N. Sedelnikov 'dans le grand lac Marka-Kul...' (item 8:128).

1914, 1916 (item 253): Material collected by Sedelnikov from 'several mountain lakes of the Altai district in the summers of 1914 and 1916' (item 253:36).

South Korea

SEIKO LAKE
1917 (item 223): Material collected from 'leaves and stems of *Trapa natans* received from Chosen (Korea)...' from 'Seiko lake near Suigen, II, 1917' and received by Skvortzov from the Director of the Agricultural Experimental Station, in Suigen, Keiki-Do (item 223:9). Some further taxonomic revisions are undertaken in item 406.

SEIRIORI LAKE
March–July 1926 (item 225): Collections made by Prof. Tamezo Mori 'in the lake at Seiriori near Seoul between March and July, 1926' (item 225:283). Some further taxonomic revisions are undertaken in item 330 and 406.

KOREAN STRAIT
1925–26 (item 256): Five samples obtained from Dr Yojiro Wakiya.

VARIOUS FOSSIL MATERIAL
1927 (item 292): Material received from Sigetaro Kawasaki, labelled 'diatom earth from the younger Tertiary, Bunzan-Men, Ampen-Gun, South Kankyo-Do' (item 292:9).

Japan

Honshû Island

KAMAGAIKE
2 October 1930 (item 318): 'Diatoms collected by Mr. Yoshikazu Okada in a mountain bog from Kamagaike, Mt. Kirigamine, Prov. Sinaro, Central Nippon, October 2. 1930' (item 318:53).

KIZAKI LAKE
July 1927 (item 293): Material collected by Mr K. Kiuchi (donated by Prof. T. Kawamura) from Kizaki Lake, Shinano Province. 'I have examined a hundred microscopic slides...Half a year was spent in the study of this collection' (item 293:9). Some further details are given in items 330, 404 and 405 along with some taxonomic revisions.

BIWA LAKE
No date (item 294): One tube of diatom clay from Biwa Lake, north

of Osaka. Sent to Skvortzov by Prof. Tamiji Kawamura. Further details are given in items 330, 404 and 405 along with some taxonomic revisions.

KANAZAWA OYSTER EXPERIMENTAL STATION
December 1927 (item 257): Material from Dr Juzo Hori (Kanazawa Oyster Experimental Station).

Kyûshû Island

IKEDA LAKE
January 1923 (item 306): Material from 'Ikeda Lake, Satsuma Province, Kiusiu Island, from the southern part of Nippon, collected by Dr. T. Kawamura in January, 1923' (item 306:191). Further details are given in items 330, 404 and 405 along with some taxonomic revisions.

Sea of Japan

1921–1925 (item 273): A series of collections made by the Imperial Fisheries Institute of Tokyo, Japan from the Sea of Japan and donated to Skvortzov by Dr K. Okamura. The collections were made on 10 July 1921, 14 November 1923, 24 November 1925 and 21 December 1925.

Wamura, Nagano Prefecture (Honshu) **(item 298)** *and Saga Prefecture (Kyushu)* **(item 299)**

VARIOUS FOSSIL MATERIAL. Skvortzov examined several samples of Neogene diatoms received from Prof. Tamij Kawamura. Item 406 is a summary article with some taxonomic revisions. Ueyama & Kobayashi (1983) have studied material from Wamura and re-assessed Skvortzov's work.

North America

January 1936 (item 295): Material from 'the Field Museum of Natural History at Chicago. The material was obtained by filtering Lake Michigan water from the city mains of Chicago in January, 1936...Type material of new forms is in the author's personal collection' (item 295:652).

Australia (Fossil)

Item 301: Material from New South Wales '...situated five miles from Cooma, and one and a half miles from Bunyan Platform...' sent by Mr F.S. Mance of the New South Wales Department of Mines, Sydney (item 301:175).

New Zealand

Item 319: Material from a series of collections sent over a period of years. The notes suggest 12 different localities.

Item 320: Material received from Mr Ian C. Edmundson, 'The sample consists of greenish masses of immense growth of *Scenedesmus brasliensis* Bohlin' (item 320:411), collected from an aquarium.

Philippines

29 January 1936 (item 309): Sample sent by Dr Eduardo Quisumbing (curator of the Phillippine National Herbarium, Manila), 'based on a sample collected January 29, 1936, from filter No. 8 in Balara, Rizal Province' (item 309:287).

Africa

1936 (item 330): Material is noted only in the review article (item 330), both localities collected by F. Pringle: 'Africa australis, in stratum lacustre prope Franzenkop et Pieska, Cape prov.' and 'Hab. Africa australis, prope Port Elizabeth, epiphytice in lichenes F. Pringle, 27/5 1936.'

Cuba

1936 (item 330): Material noted only in the review article (item 330). Both localities collected by Rev. B. Robert: 'Hab. America australis, Cuba, Habana, prope Vedado, epipytice apud radices' and 'Hab. America australis, Cuba, Habana, prope Vedado, epipytice in truncos arbores. Rev. B. Robert, 40/6 1936'.

Afghanistan

1916 (item 4): Material collected by Mr V. Lagatov 'dans les canaux de Mourgab prés de la frontiére d'Afghanistan et de Perse dans le desert sablonneux de Kara-Koum' (item 4:19).

Sri Lanka

1926 (item 235): Material from several collections made by A.H.G. Alston. Much of Alston's material is in the BM. A search, so far, has revealed nothing of direct relevance.

1926 (item 265): Material collected by A.H.G. Alston, 'near the sea shore at Gintota from the twigs of *Ceramium clavulatum*' on the 16 August 1926.

No date (items 330 & 361): Material donated by Dr N.G. Ball 'in a swamp in mountain region'.

India

February 1926 (item 288): Two samples from Prof. S.R. Bose; one from mosses and algae from tree bark (15 Feburary 1926), the other from mud in a channel.

B.V. SKVORTZOV'S BIBLIOGRAPHY

As far as we are aware this is a complete listing of Skvortzov's published work. It is probable that some other publications may be in inaccessible natural history journals and magazines printed in Manchuria. The authorship is Skvortzov unless otherwise stated. An asterisk (*) denotes a publication that includes diatom species. We have not seen the last six entries in this list and presume they were published posthumously.

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2. **Skvortzov, B.V.** 1917. Über Flagellata aus Mandschurei. Part 1. *Zhurnal Mikrobïologiï* **4** (1–2): 57–78. (French summary p. 287).
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12. —— 1918. On little known vegetable tuber plants of Manchuria. *Sel'skoe Khoziaïstvo v Sievernoï Man'chzhurii* **5–6**: 26. (In Russian).
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On the identity of *Pleurosigma angulatum* (Bacillariophyta) and related species

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CONTENTS

SYNOPSIS. The specific status of *Pleurosigma angulatum* (J.T. Quekett) W. Sm. is clarified. *P. angulatum*, *P. quadratum* W. Sm. and *P. aestuarii* (Bréb.) W. Sm. are shown to be separate taxa. Recent research has subsumed the three taxa under the epithet *angulatum* on the basis that they may occur together and so may represent different stages in the life cycle of one species. The results of this study show this is clearly not the case.

Two new species of *Pleurosigma* are described; *P. mamoranqi* **sp. nov.** from New Zealand and *P. lysekilii* **sp. nov.** from Sweden. One new name, *P. malmoensis* **nom. nov.**, is given to the taxon previously called *Pleurosigma minutum* (Grun.) Cl.

INTRODUCTION

The genus *Pleurosigma* W. Sm. is a member of the family Pleurosigmataceae. *Pleurosigma* is a readily recognized genus owing to its large size, sigmoid outline or sigmoid raphe, and its arrangement of transverse and oblique striae. It has two or four ribbon-like plastids which undulate throughout the cell. Initially, species of *Pleurosigma* were distinguished largely on the basis of their shape (Kützing, 1833; Ehrenberg, 1838; Rabenhorst, 1853).

Smith (1852) used the new name *Pleurosigma* W. Sm. for sigmoid naviculoid diatoms; his reason for rejecting the earlier name *Gyrosigma* Hassall, which was in his view synonymous with *Pleurosigma*, was that it was an 'alliterative blunder' (Smith, 1856: 97). Smith (1852) introduced additional taxonomic criteria in this group of diatoms by separating species into two 'sections' on the basis of the arrangement of the striae. He also provided details of the stria density for each species and used this as the basis for discriminating between them. Smith's (1852) two sections reflected the modern concepts of *Gyrosigma* and *Pleurosigma*, his first section being described as having 'Beads alternate, striae oblique', i.e. *Pleurosigma* (Round et al., 1990), whereas his second section had 'Beads opposite, striae transverse and longitudinal', i.e. *Gyrosigma* (Round et al., 1990).

Peragallo (1891) investigated the angle of intersection of the striae in taxa of the family Pleurosigmataceae. By combining the angle of intersection and fineness of the striae, he was able to discriminate additional species and divide them into 11 groups; *Pleurosigma* was still included within *Gyrosigma* at this point. Cleve (1894) later separated *Gyrosigma* from *Pleurosigma* using the orientation of the striae and assessed species limits within the genera by the shape and path of the raphe.

Pleurosigma angulatum (J.T. Quekett) W. Sm. was conserved as the type of the genus *Pleurosigma* by Ross (during the 8th International Botanical Congress, Paris, 1954). *P. angulatum* has been treated in a variety of ways encompassing a large number of varietal forms (16 listed in Reid, 1998). It was first described by Quekett (1848:438) as *Navicula angulata* from 'the Humber at Hull'. Recent work by Sterrenburg (1991*a*) and Ross & Sterrenburg (1996) argued that *P. angulatum* be extended to encompass *P. angulatum*, *P. quadratum* W. Sm. and P. *aestuarii* (Bréb.) W. Sm. This was based on the assumption that they are all part of the same species, just exhibitions of different stages in the 'vegetative cycle of a single organism; *quadratum* as early stage, *angulatum* representing mid-range and *aestuarii* as late stage' (Sterrenburg, 1991*a*: 564). Searches for Quekett's original material failed to locate any specimens and resulted in the proposal to conserve the name *P. angulatum* (J.T. Quekett) W. Sm. with a conserved type slide from the Wm. Smith collection (BM 23671) (Ross & Sterrenburg, 1996).

In a detailed monographic study of the genus *Pleurosigma*, Reid

(1998) disagreed with Sterrenburg's findings. Her results showed that *P. angulatum, P. quadratum* and *P. aestuarii* should be recognized as separate taxa. This study extends Reid's (1998) findings using cladistic analyses to explore the relationships of the three taxa and their close relatives as indicated from Reid's results.

MATERIALS & METHODS

Slides were examined using a Reichert microscope. For photomicroscopy, specimens were examined on a Carl Zeiss microscope, with differential interference contrast, using plan apochromat objectives and tri colour green filter. Photos were taken using medium format Kodak Tmax 100 film. Cleaned specimens were strewn on aluminium stubs for SEM examination. The specimens were sputter coated with platinum and observed using a Hitachi S800 field electron microscope. All slides, negatives and SEM stubs of the specimens are housed in the herbarium of The Natural History Museum, London (BM).

Diatom morphology

Terminology for the siliceous parts of the diatom frustule follows that of Anon. (1975) and Ross et al. (1979).

Characters that appeared constant within species were investigated using cladistic analysis. Character stability was established by investigating about ten populations from each taxon (examining more than 100 individuals from each population) for infra- and interspecific variation. Individuals were cultured from each population and subjected to variations in temperature (9–30°C), salinity (7–43 ppt) and light (8–45 µmol m^{-2} sec^{-1}) to assess character stability under a multifactorial design. All characters were measured in both the 'wild' and the 'cultured' material.

Only qualitative characters were used in the cladistic analysis. Quantitative characters were not used due to the inherent problems of coding continuous characters into discrete states for analysis (Pimentel & Riggins, 1987; Thiele, 1993; Reid & Sidwell, 2001). Many characters traditionally associated with diatom valve morphology are quantitative (e.g. length, breadth, stria ratios) and only used in species descriptions. The only characteristics of shape that can be used qualitatively are first, the broad definition of cells as arcuate (as in the outgroup *Toxonidea* Donkin, compared to sigmoid cells as in the remaining Pleurosigmataceae), and second, shape in girdle view (oblong in *Pleurosigma* and panduriform in *Donkinia*).

Within the family Pleurosigmataceae the striae are arranged in one of two ways; transverse and oblique rows in *Pleurosigma, Toxonidea* and *Donkinia*, longitudinal and transverse rows in *Gyrosigma* and *Donkinia*. This character was first used to separate *Gyrosigma* and *Pleurosigma* into two distinct genera by Cleve (1894). The areolae in the Pleurosigmataceae are loculate and occluded by a rica. The areolae open externally by a slit, the foramen. The internal areola opening in the Pleurosigmataceae can be divided into two types; either a single opening which is found in *Gyrosigma, Toxonidea*, some species of *Pleurosigma* (Fig. 3c) and *Donkinia*, or areolae divided by a siliceous bar, as found in some species of *Pleurosigma* and *Donkinia* (Fig. 5c). In some species of *Pleurosigma* the striae change orientation near the apex of the valve from the transverse/oblique pattern to the transverse/longitudinal pattern (Fig. 3f). This change was first noted and clearly drawn and discussed by Anthony (1870). Sterrenburg attributed this discovery to Hendey (1964), commenting that 'this had never been described or drawn in the previous century of observations' (Sterrenburg, 1991*a*:561). This is not the case, as it had been commented on frequently in the literature prior to Hendey, for example Brown (1914:327) regarded this as 'a good specific character', and Woodward (1871:160) made detailed photographic illustrations of the character.

The external central raphe fissures of *Pleurosigma* were first discussed as a taxonomic character by Cardinal et al. (1989). These are continuations of the external raphe slit opening, extending onto or across the central nodule, but not penetrating the valve. This character refers to the orientation of the central external raphe fissure endings (see Fig. 2g). Cardinal et al. (1989) used six character states in their study, only four of these are seen in the species under investigation here: either the central fissures are curved in opposite directions, similar directions, one centered and the other deflected, or the central fissures are overlapping.

Central bars are siliceous thickenings deposited either side of the internal central nodule (Fig. 2f). Reid (1998) observed eight character states in her study, four of which are observed in the species under investigation here: central bars smooth and slender, with an indistinct hazy edge, with siliceous lateral extensions or thick and raised. A hyaline area may occur adjacent to these bars (this is an area which is not penetrated by areolae) and may follow the shape of these bars (Fig. 3h) or be transversely expanded (Fig. 5c) or absent (Fig. 2f). In some species of *Pleurosigma* the internal central area is raised to form a 'saddled' humped area. The internal central nodule may have an extra siliceous deposit in the centre in some species of *Pleurosigma* (Fig. 5c), a character referred to as 'central nodule raised' in the cladistic analysis.

Analysis

Table 1 lists the characters and the character states used in the analysis; character coding is presented in Table 2. The data set

Table 1 Characters and character codes used in the cladistic analysis

Character	Character Description	Character code
0	Valve arcuate	0
	Valve sigmoid	1
1	Striae transverse and oblique	0
	Striae transverse and longitudinal	1
2	Raphe arcuate	0
	Raphe sigmoid	1
3	Areolae undivided	0
	Areolae divided	1
4	Striae same orientation at apex	0
	Striae change orientation at the apex	1
5	Central raphe fissures:	
	Curved in same direction	0
	Curved in opposite directions	1
	One centred the other deviated	2
	Overlapping	3
6	Central area not saddled	0
	Central area saddled	1
7	Central bars:	
	Smooth and slender	0
	With indistinct hazy edge	1
	With siliceous lateral extensions	2
	Thick and raised	3
8	Hyaline area:	
	transversely expanded	0
	follows the central bars	1
	absent	2
9	Central nodule raised	0
	Central nodule plain	1
10	Valve flat	0
	Valve vaulted	1
11	Girdle view oblong	0
	Girdle view paduriform	1

Table 2 Data matrix used in the cladistic analysis

	0	1	2	3	4	5	6	7	8	9	10	11
Toxonidea	0	0	0	0	0	0	0	0	0	0	0	0
P. angulatum	1	0	1	0	1	2	0	1	2	0	0	0
P. quadratum	1	0	1	0	1	2	0	1	1	0	0	0
P. aestuarii	1	0	1	0	1	3	0	0	2	1	0	0
P. stidolphii	1	0	1	0	0	3	0	2	0	1	1	0
P. mamoranqi	1	0	1	1	0	3	0	0	0	0	0	0
P. lysekilii	1	0	1	?	0	0	0	0	?	?	0	0
P. malmoensis	1	0	1	?	0	0	0	0	?	?	0	0
P. rhombeum	1	0	1	0	0	1	1	0	0	0	1	0
D. minutum	1	1	1	0	0	?	0	3	1	1	1	1
D. latum	1	1	1	0	0	?	0	3	1	1	1	1

contains ten binary characters and two multistate characters, which were coded with reference to *Toxonidea* as an all zero outgroup (Nixon & Carpenter, 1993).

Pleurosigma minutum Donkin (not to be confused with *Pleurosigma minutum* Grun.) is synonymous with *Donkinia minutum* (Donkin) Ralfs. As *Donkinia* is seemingly closely related to *Pleurosigma*, two species in the genus, *D. minutum* and *D. latum* E.J. Cox, were included in the analysis. *P. rhombeum* Grun. was included in the analysis because this is a taxon which is often misidentified as *P. quadratum*.

Weighting is the importance applied to characters in analysis. When different characters are assumed to contribute to the same degree to the tree topology they are all given the same weight (uniform weighting), applied initially as the default in most current parsimony programs (e.g. Hennig86 – Farris, 1988; PAUP – Swofford, 1990). If the characters are assumed to contribute to different extents to the analysis they are given different weights (differential weighting).

In the past, weighting has tended to be a highly subjective process with intuition being the only basis for giving some characters more weight than others in an analysis (e.g. Mayr, 1969). Weighting may take place prior to tree construction, in which case it is termed *a priori* weighting (Neff, 1986), which takes into account what is known about the characters, or after initial tree construction, in which case it takes into account the contribution the characters make to the resulting tree topology, *a posteriori* weighting (Neff, 1986). *A priori* weighting is not appropriate as it is impossible to know which characters are useful before an analysis.

The first serious attempt to address the problem of how to weight characters was brought about by Farris (1969), but little use was made of it until he incorporated it into his computer program (Farris, 1988), as a differential *a posteriori* method. The method is based on the assumption that 'characters which have failed repeatedly to adjust to the expectation of hierarchic correlation are more likely to fail again in the future, and so they are less likely to predict accurately the distribution of as yet unobserved characters' (Goloboff, 1993*a*). In practice this is the same as excluding some characters and introducing the non-random replication of other characters. Farris's method (Farris, 1969, 1988) is iterative in that weights are applied to the most parsimonious trees for a given set of weights, and are then used in the reanalyses. It works on the basis that because the character consistency index (c) measures homoplasy but can never reach zero, by rescaling it with the retention index (ri) (which measures the amount of synapomorphy), characters with no synapomorphy can be disregarded in future analyses.

Goloboff (1991*a*) shows that Farris's method of weighting still has problems as weights do not always increase with less homoplasy. Goloboff (1993*b*) introduced a non-iterative method in which the weighting is based on a concave function of homoplasy, given as fit (f):

$$f = (k+1) / (s+k+1-m)$$

k = a constant of concavity, s= minimum number of steps a character can have on a particular tree, m= minimum number of steps a character can have on any tree. This is implemented using the computer program Pee-Wee (Goloboff 1993*b*) to analyse the data matrix. It selects trees of highest weight as being the most parsimonious, as opposed to the shortest total length, as under Hennig86 (Farris, 1988).

Some workers only advocate the use of weighting in the analysis if the initial unweighted data has failed to produce an adequate tree due to character conflict, or to choose between multiple trees (Turner & Zandee, 1995; Rodrigo, 1992). This approach is rejected here because weighting selects characters not cladograms. Many workers do not accept the concept of differential character weighting, arguing that every character should be attributed equal weight to create natural taxa because all characters are 'equally desirable' (Sneath & Sokal, 1973; Mann, 1982; Round et al., 1990). I shall use differential *a posteriori* weighting because it results in trees which are self-consistent with the data collected (Farris 1969, 1988; Goloboff, 1993*a*, 1995; Platnick et al., 1991), in that not all characters contribute equal amounts of information to the analysis. They are given the weight they deserve after initial analysis and thus weighting is required in all analysis.

Parsimonious trees for the data were found using Hennig86 (Farris, 1988) with the *ie** command (implicit enumeration, which is guaranteed to find all the most parsimonious trees). Initially, all characters were given equal weight and were unordered. As it is possible that not all characters contribute to the same extent to the prediction of relationships (Farris, 1983; Goloboff, 1993*a*), *a posteriori* differential weighting was investigated (as implemented in the program Pee-Wee (Goloboff, 1993*b*)). The option *mult*50* was used to search for trees of highest fit, performing random addition sequences of 50 replications each. Replication was followed by tree bisection and branch-swapping.

RESULTS

Both Henning86 and Pee-Wee resolved the same tree (length 19, ci 89, ri 88, fit 75 (Fig. 1)). The tree in Fig. 1 has seven nodes (labelled 0–6, with 0 the most basal node of the tree).

Pleurosigma angulatum and *P. quadratum* are resolved at node 4 supported by character 5 (central raphe fissure orientation) and character 7 (central bar type). Node 2 resolves *P. aestuarii* as sister taxon to these two taxa supported by character 4 (striae orientation at apex) and character 8 (hyaline area type). The resolution at node 3 (*P. rhombeum, P. stidolpii, D. minutum* and *D. latum*) is attributed to character 10 (valve vaulting). The resolution at node 5 (*P. stidolpii, D. minutum* and *D. latum*) is based on character 9 (central

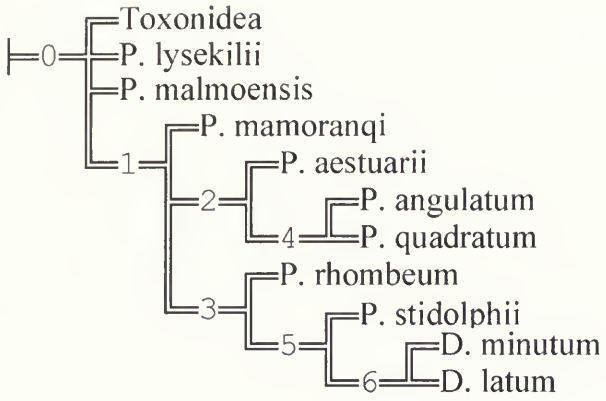

Fig. 1 Tree resolved by Hennig86 and Pee-Wee. Numbers on braches indicate the nodes

Table 3 Character weights

Character	Fit	Character	Fit
0	/	6	/
1	10	7	10
2	/	8	7.5
3	/	9	7.5
4	10	10	10
5	10	11	10

nodule type) and at node 6 (*D. minutum* and *D. latum*) based on character 1 (striae orientation), character 8 (hyaline area type) and character 11 (girdle view shape).

Weights attributed to the characters were high suggesting that they are relatively reliable (Table 3). Six characters received the maximum weight of 10, indicating that the characters were performing well and were hierarchically correlated. Two received a value of 7.5, which also indicates a high level of correlation. Characters 0 and 2 do not receive a weight because they only serve to separate the ingroup from the outgroup. Characters 3 and 6 do not receive a weight as they are autapomorphic.

DISCUSSION

Sterrenburg (1991*a*: 561) stated that 'There is no morphological discontinuity between *Pleurosigma quadratum* W. Sm., *Pleurosigma angulatum* sensu W. Smith and *Pleurosigma aestuarii* (Bréb. *ex* Kütz.) W. Smith and the species description of *Pleurosigma angulatum* is extended to account for this continuum.' However, detailed morphological studies of large numbers of specimens has shown that this is not the case and that they are separate taxa.

The taxa differ in their hyaline areas; *Pleurosigma angulatum* and *P. aestuarii* do not have one (Figs 2f & 4c) whereas in *P. quadratum* the hyaline area follows the central bars (Fig. 3h). The taxa differ in their central bars, with *P. quadratum* having extra thickening at the centre of the bar (Fig. 3h) whereas *P. angulatum* has a more even deposit of silica (Fig. 2f) and *P. aestuarii* has smooth slender bars (Fig. 4b). *P. quadratum* is a much larger taxon than *P. angulatum* with a distinctive rhomboidal shape, compared to the more lanceolate form of the latter species. *P. aestuarii* is much smaller with rostrate ends. *P angulatum* possesses a different pattern change at its apices to *P. quadratum* and *P. aestuarii*. On the outside curve of the raphe the pattern continues approximately twice as far as on the opposite side (Figs 2h–j), whereas in *P. aestuarii* and *P. quadratum* the change in stria orientation is equal on both sides of the raphe (Figs 3b, c, f & 4c). Due to these differences they are maintained as separate taxa.

The basis for Sterrenburg's (1991*a*) summation is that the taxa are frequently found together. In this study, examination of many different populations showed that this is not the case, with their only occasionally being found together. While in nature many taxa frequently occur together, this is no basis for assuming that they are all to be regarded as one taxon; they may just have similar environmental requirements. Sterrenburg (1991*a*: 564) considers that there is 'a biological continuum between *quadratum, angulatum* and *aestuarii*'. Yet he admits that 'some samples may be almost pure *aestuarii*', continuing that 'While this may suggest the taxon's individuality, it does not necessarily imply it'. Reid (unpublished data) grew populations of *Pleurosigma angulatum* under different environmental conditions and monitored their morphometric changes. She found no evidence to support Sterrenburg's hypothesis.

Sterrenburg (1991*a*: 563) states that 'central bars were found to be highly variable in several of the "states" defined and discussed in Cardinal et al. (1989).' This found central bars to be a stable character both within a population and between populations from different sites. As Sterrenburg is subsuming the taxa under one species this may account for the variability he is observing. Sterrenburg (1991*a*) also sees the three taxa as part of a size range continuum. If this is the case, why is there a complete size range for each species that can clearly be seen to belong to each nominate type? Examination of large populations from different locations reveals the range in variation, but each taxon can still be clearly recognized.

Sterrenburg (1991*a*) suggested that Queckett (1848) had illustrated two taxa because his illustrations show one taxon with 51° and one with 60° angle of stria intersection. However this does not necessarily imply the inclusion of two different taxa, because this range of angles can be found in *Pleurosigma quadratum,* which exhibits angles from 50–60°. This is a continuous character, which cannot be fitted into discrete character states. Sterrenburg (1991*a*) refutes this possibility as 'Stria angle was found to be a stable parameter in this genus in Sterrenburg 1991 and the findings then indicated that 51 deg. falls outside the range of variation for *Pleurosigma angulatum* sensu W. Smith.' (Sterrenburg, 1991*a*:561). These observations were made on only two populations, one from the Wadden Sea, Holland and one from New Zealand (Sterrenburg 1991*b*:371) so it is quite likely that the full range of variation was not observed, giving him only 57–62°.

However, the results of the systematic analysis do show these taxa to be closely related. *Pleurosigma angulatum* and *P. quadratum* are resolved in both the unweighted and the weighted analyses as sister taxa (Fig. 1) at node 4 supported by character 5 (central raphe fissure orientation) and character 7 (central bar type). *P. aestuarii* is shown to be their closest relative at node 2 supported by characters 4 (striae orientation at apex) and 8 (hyaline area type). The shift in orientation at the apex was discussed by Reid (1998) and has been shown to be a stable taxon-specific character within the genus *Pleurosigma*. This character is a very useful aid to the identification of this complex group as it is easily visible under the light microscope and is shown by only 15 members of the genus. It does not change under environmental conditions or during growth.

No unmounted material was available for SEM investigation of *Pleurosigma lysekilii* Reid and *P. malmoensis* Reid, therefore characters 3 (areolae type), 8 (hyaline area type), and 9 (central

nodule type) are scored as '?' in the cladistic analysis, leaving them unresolved within the group at node 0 of the tree (Fig. 1).

Pleurosigma mamoranqi Reid differs from *P. angulatum, P. quadratum* and *P. stidolphii* Sterrenburg in having areolae crossed by a bar. It differs from *P. angulatum* and *P. quadratum* by its striae that do not change orientation near the apex. It has a large expanded hyaline area adjacent to the central bars. It differs from *P. rhombeum* by not having a saddled central area. This taxon does not fit any of the previously published descriptions of *Pleurosigma,* and as such is described as new.

In the first part of his monograph Peragallo (1891:12) considered *Pleurosigma minutum* to be a valid taxon and expands its distribution from Malmö, Sweden to include the Balearic Islands. However, in the second part of his monograph, Peragallo (1891:34) considers *P. minutum* as a doubtful or unknown species. He says 'Je n'ai pu l'identifier avec certitude.' (Peragallo, 1891:34). The present study shows that *P. minutum* is a valid taxon that can be clearly distinguished from other species of *Pleurosigma. P. minutum* is quite different to *Donkinia minutum* which has a highly vaulted valve with its raphe on a keel. It is panduriform in girdle view whereas *P. minutum* is rectangular. *P. minutum* has transverse and oblique striae whereas *D. minutum* has transverse and longitudinal striae. However, as the name *P. minutum* had been used prior to Grunow (*P. minutum* Donkin, 1858:24, 3/9) a new name, *P. malmoensis*, is proposed for this taxon. *D. minutum* was not shown to be closely related to *P. malmoensis*, being placed in a different part of the tree, and therefore they cannot be considered as the same taxon.

TAXONOMIC TREATMENT

1. **Pleurosigma angulatum** (J.T. Quekett) W. Sm. in *Ann. Nat. Hist.* **9**: 7, pl. 1 fig. 8 (1852) Type: England, Hull, Humber Estuary (Lectotype: Belfast, 1996, *Ross & Sterrenburg* BM 23671!).

Fig. 2

Navicula angulata J.T. Quekett in *A practical treatise on the use of the microscope:* 438, pl. 8 fig. 4–7 (1848).

Pleurosigma angulatum f. *minor* Rabenh., *Flora Europea Algarum*: 234 (1864).

Pleurosigma angulatum var. *robustum* McCall, *J. Linn. Soc., Botany* **49**: 265, 306 (1933).

Valve rhomboidal sigmoid, length 120–280 µm, breadth 30–35 µm (Figs 2a–d). Raphe sigmoid, central, becoming slightly eccentric near the apices (Figs 2a–d). External central raphe fissures with one centred and the other deflected to one side (Fig. 2g). Hyaline area absent (Fig. 2e, f). Striae 20 per 10 µm, crossing at an angle of 54–60°. Striae change orientation at the apex, the pattern change continues about twice the distance on the outer most curve of the raphe compared with the inner side (Figs 2h–j). Areolae undivided. Central bars of approximately equal length with an indistinct outer edge (Fig. 2f).

Ross & Sterrenburg (1996) chose to conserve BM 23671 as the type of the species. They record it as 'Belfast, August 1849', and state that this slide is from a locality listed in Smith (1853:65) 'Poole Bay, Aug. 1848; Belfast Bay, Aug. 1849; Coast of Sussex, April, May and Aug. 1852, *W. Sm.* Coast of Lancashire, *Mr. Johnson.* Rye, *Mr. Jenner.* Hull, *Mr. R. Harrison.* Coast of Norfolk, *Mr. Brightwell*'. This is somewhat misleading because in his earlier work, when he originally described *P. angulatum*, Smith (1852) gave the locality as Belfast Bay, Liverpool not Belfast (Ireland). The choice of locality is also somewhat strange as Quekett's (1848) original description is of a taxon found 'upon conferva in the Humber at Hull'. From the list in Smith's (1852) description ('Poole Bay; Belfast Bay, Liverpool; Coast of Sussex, &c.; Coast of Lancashire, *Chr. Johnson, Esq.*! Rye, *Mr. Jenner*! Hull, *Mr. R. Harrison*! Norfolk, *Thos. Brightwell Esq.*!' (Smith 1852:7)) a Hull sample would have been a more judicious choice, for example BM 11809 and BM 11810 both from Hull and collected by *R. Harrison*. The slide (BM 23671) has unfortunately been damaged by someone circling the specimen of *P. angulatum* and this has caused a perforation in the coverslip which has led to the slide drying out.

The taxon described by McCall (1933) as *Pleurosigma angulatum* var. *robustum* (Fig. 2d) is subsumed under the name *P. angulatum* as no morphological differences can be found.

MATERIAL EXAMINED

UNITED KINGDOM. England. Hartlepool, n.d., *Arnott* 570, Greville Coll. (BM 96); sine loc., n.d., *Wm. Smith* 2, Greville Coll. (BM 204); Hull, 1856, *G.N.* s.n., Greville Coll. (BM 386); Blyth Harbour, November 1857, *Donkin* C. No. 1, Greville Coll. (BM 389); Harwich, n.d., *Anon.* Deby Coll. (BM 7251); Harwich, n.d., *Anon.* Deby Coll. (BM 7253); Hull, n.d., *R. Harrison* 117, Deby Coll. (BM 11809); Hull, n.d., *R. Harrison* 117, Deby Coll. (BM 11810); sine loc., n.d., *W.S.* 205, Deby Coll. (BM 13331); Norfolk, n.d., *F. Kitton* 43, Deby Coll. (BM 13703); Poole Bay, August 1849, *Anon.*, Wm. Smith Coll. (BM 23672); Pevensey, September 1851, *Anon.*, Wm. Smith Coll. (BM 23674); Sussex, Ilford, April 1852, *Anon.*, Wm. Smith Coll. (BM 23675); Sussex, Lancing, August 1852, *Anon.*,Wm. Smith Coll. (BM 23676); Sussex, Seaford, December 1852, *Anon.*, Wm. Smith Coll. (BM 23677); Pevensey, August 1853, *Anon.*, Wm. Smith Coll. (BM 23679); Sussex, Newhaven, February 1854, *Anon.*, Wm. Smith Coll. (BM 23681); Sussex, Southease, August 1854, *Anon.*, Wm. Smith Coll. (BM 23682); Sussex, Shoreham, April 1854, *Anon.*, Wm. Smith Coll. (BM 23683); Sussex, Shoreham, April 1854, *Anon.*, Wm. Smith Coll. (BM 23684); Essex, Walton, n.d., *Comber* 3 (BM 31459); Essex, Walton, n.d., *Comber* 2 (BM 31458); Den Marsh, May 1896, *Comber* s.n., (BM 31460); Den Marsh, May 1896, *Comber* s.n., (BM 31461); Kent, Broad Water, near chalk 'S.157, 326', n.d., *Rylands* s.n., (BM 48371); River Mersey, n.d., *I. Hardmach* 331, Rylands Coll. (BM 48441); River Mersey, n.d., *I. Hardmach* 331, Rylands Coll. (BM 48442); Hull, 1857, *W* 103, 331, Rylands Coll. (BM 48444); Humber, Hull, n.d., *GN* 103, Rylands Coll. (BM 49989); Humber, Hull, n.d., *GN* 103, Rylands Coll. (BM 49990); Humber, Hull, n.d., *GN* 103, Rylands Coll. (BM 49991); Humber, Hull, n.d., *GN* 103, Rylands Coll. (BM 49992); Lancaster, Salt pool, '(274)383', n.d., *Rylands* s.n., (BM 48593). **Scotland**: Fife, Tayport, Tents Muir, Brackish Burn, n.d., *D.R. McCall* s.n. (BM 83451); Tayport, mud scraping from brackish pool on links, 23 September 1916, ex *A.W. Round* s.n., , J.R. Carter Coll. (BM 93648). **Northern Ireland**: Belfast, Queens Island, n.d., *Arnott* 655, Greville Coll. (BM 1648); Belfast, August 1849, *Anon.*,Wm. Smith Coll. (BM 23671); Carrickfergus, August 1849, *Anon.*, Wm. Smith Coll. (BM 23673).

IRELAND. Galway, July 1853, s.n., Wm. Smith Coll. (BM 23678).

FRANCE. sine loc. 'Diatomées de France', n.d., 33/2,3 *Anon.*, (BM – Adams Coll.).

2. ***Pleurosigma quadratum*** W. Sm., in A *synopsis of the British Diatomaceae.* **1**: 65 pl. 20 fig. 204 (1853). Type (designated here): England, Sussex, August 1850, *Anon.*, BM 23669! (Isotype localities: Poole Bay; Coast of Sussex; Devonshire; Menai Straits; Folkestone).

Fig. 3

Pleurosigma angulatum W. Sm., *Ann. Nat. Hist.* **9**: 7, pl. 1 fig. 7 & 9 (1852).

Pleurosigma angulatum var. *quadratum* (W. Sm.) Van Heurck, *Synopsis Diatomées Belgique*: 115 (1885).

Valves strongly rhombic, sigmoid, length 130–285 µm, breadth 50–65 µm (Fig. 3a, d). Raphe sigmoid eccentric towards the apices (Fig. 3a, d). Areolae undivided (Fig. 3c), transverse striae 19 per 10 µm,

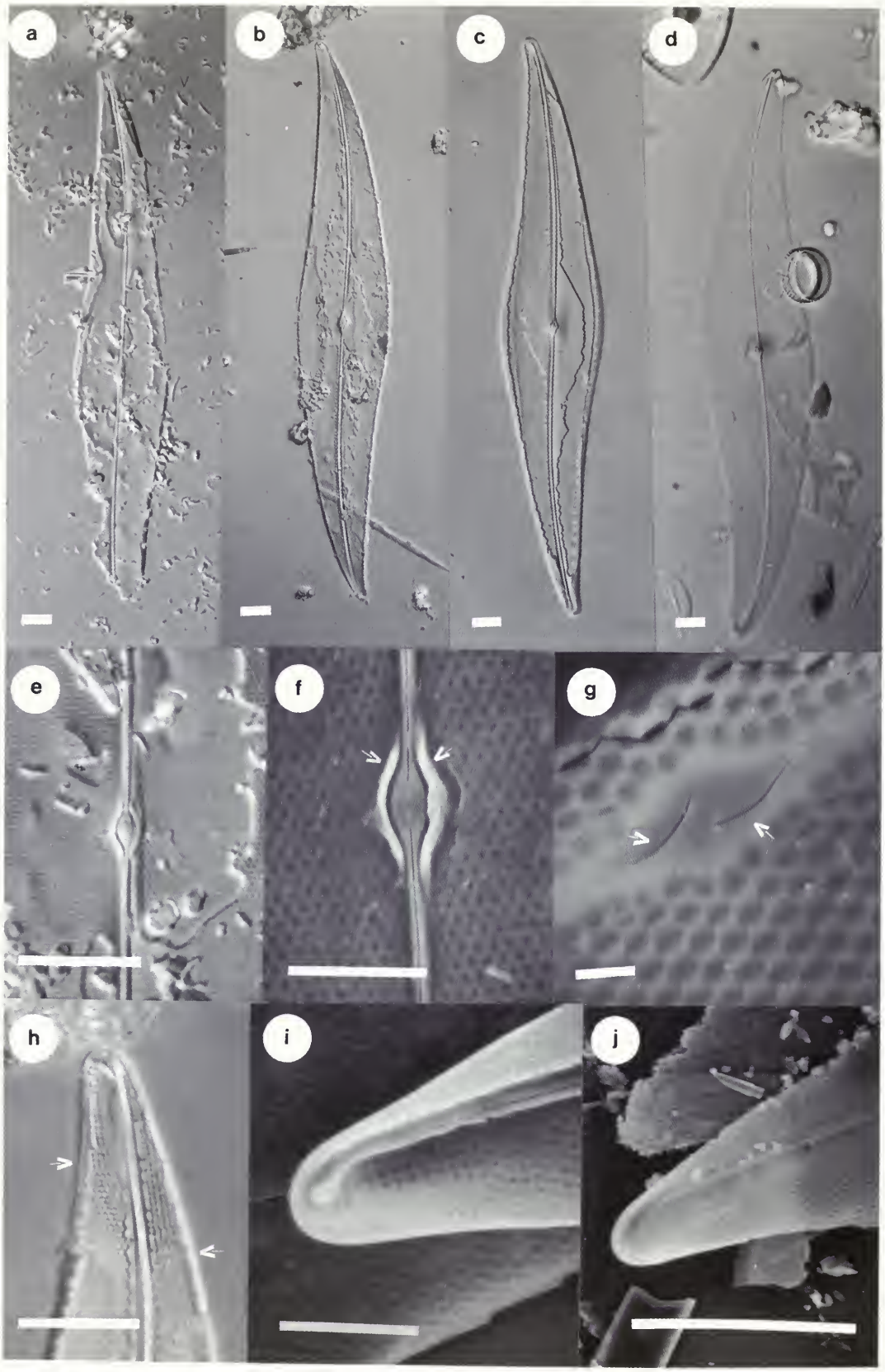

Fig. 2 ***Pleurosigma angulatum.*** (a) BM 23671; (b) BM 23674; (c) BM 386; (d) *P. angulatum* var. *robustum* (BM 83451); (e) light micrograph of central area (BM 23671); (f) SEM of internal central area, arrows indicating central bars; (g) SEM of external central fissures (arrows), one centred the other deflected; (h) light micrograph of valve apex showing change in striae orientation, arrows indicating the different distance of the striae change on either side of the raphe (BM 23674); (i) SEM of internal valve apex; (j) SEM of external valve apex. SEM micrographs from material of Wm. Smith Herbarium, *Anon.,* Sussex, Lancing, August 1852. (Scale bars: a–e, h & j = 10 µm, f & i = 5 µm; g = 1 µm).

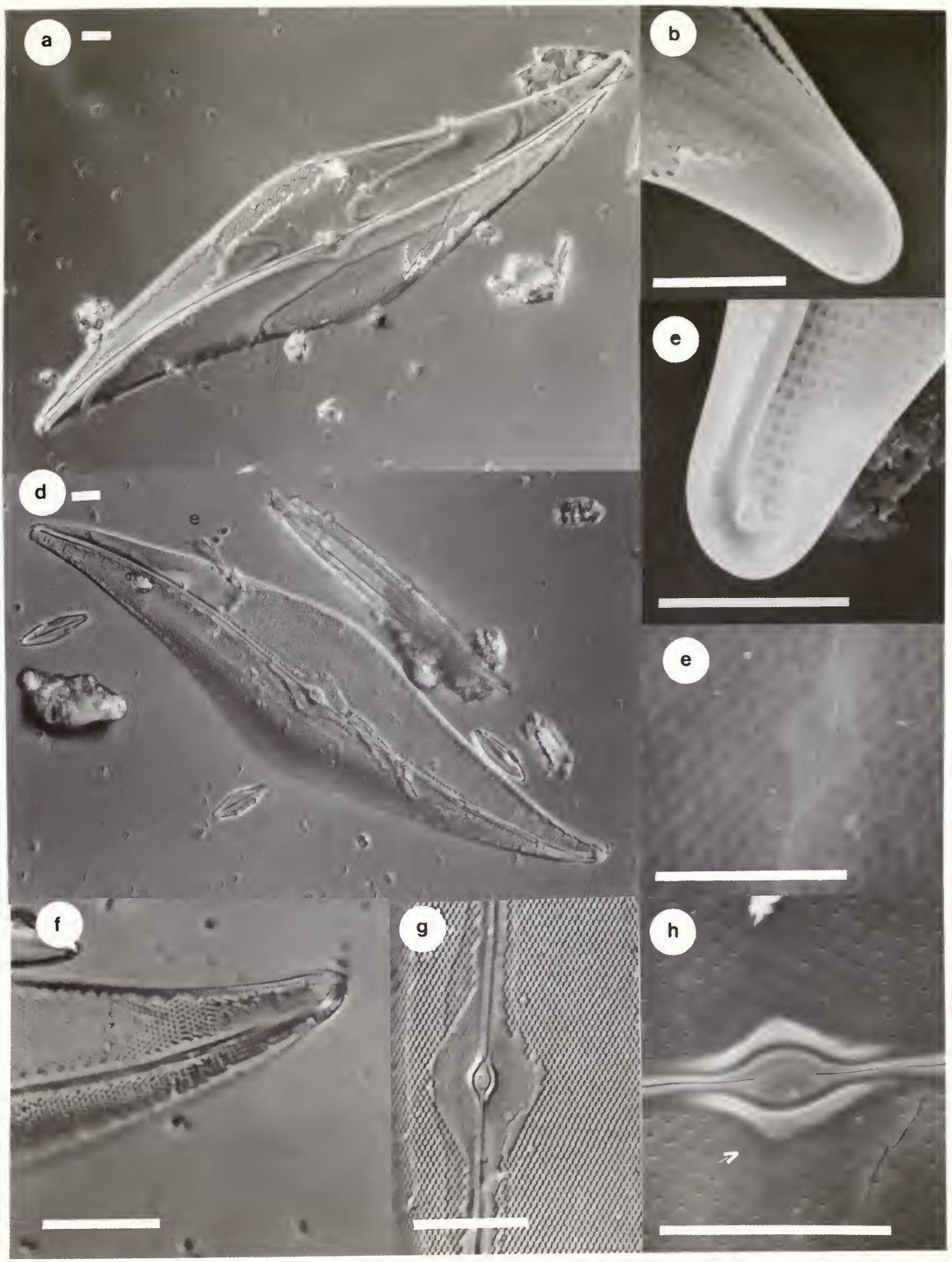

Fig. 3 ***Pleurosigma quadratum.*** (a) BM 23669; (b) SEM of external apex; (c) SEM of internal apex; (d) BM 23669; (e) SEM of external central area showing central raphe fissures; (f) light micrograph of valve apex showing change in striae orientation (BM 23669); (g) light micrograph of central area (BM 23669); (h) SEM of internal central area, arrow indicating hyaline area. SEM micrographs of Wm. Smith Herbarium material, *Anon.,* Sussex, August 1850. (Scale bars: a, d, f, g = 10 μm; b, c, e, h = 5 μm).

oblique striae 18 per 10 µm, intersecting at an angle of 50–60°, changing orientation near the apex (Fig. 3b, c, f). External central raphe fissures one deviating to one side the other centred (Fig. 3e). Central bars of approximately equal length, thickened at the centre with an indistinct outer edge (Fig. 3g, h). Hyaline area follows central bars (Fig. 3h) in contrast to *P. angulatum* (Fig. 2f).

MATERIAL EXAMINED

UNITED KINGDOM. England: Harwich, n.d., *Arnott* s.n., Greville Coll. (BM 316); *W. Smith* 204, Greville Coll. (BM 219); Devon, Saltmarsh, n.d., *Gregory* s.n., Greville Coll. (BM 2129); Harwich, n.d., *A. Gr.* 814, Deby Coll. (BM 7108); Poole Bay, June 11 1849, *Smith* 204, Deby Coll. (BM 13320); Folkstone, November 1852, *J.R. Capron, Smith* 204, Deby Coll. (BM 13321); Norfolk, n.d., *F. Kitton* 43, Deby Coll. (BM 13703); test slide, sine loc., n.d., *Anon.*, Roper Coll. (BM 20751); Sussex, August 1850, *Anon.*, Wm. Smith Coll. (BM 23669); Hull, n.d., *Dr Ivl* 330/1, Rylands Coll. (BM 48384); Hull, n.d., *Dr Ivl* 330/2 Rylands Coll. (BM 48385); Northfleet (S. 750) 330, n.d., *Anon.*, Rylands Coll. (BM 88383); Harwich, Walton Ferry, n.d., *Anon.* 814, Rylands Coll. (BM 50436).

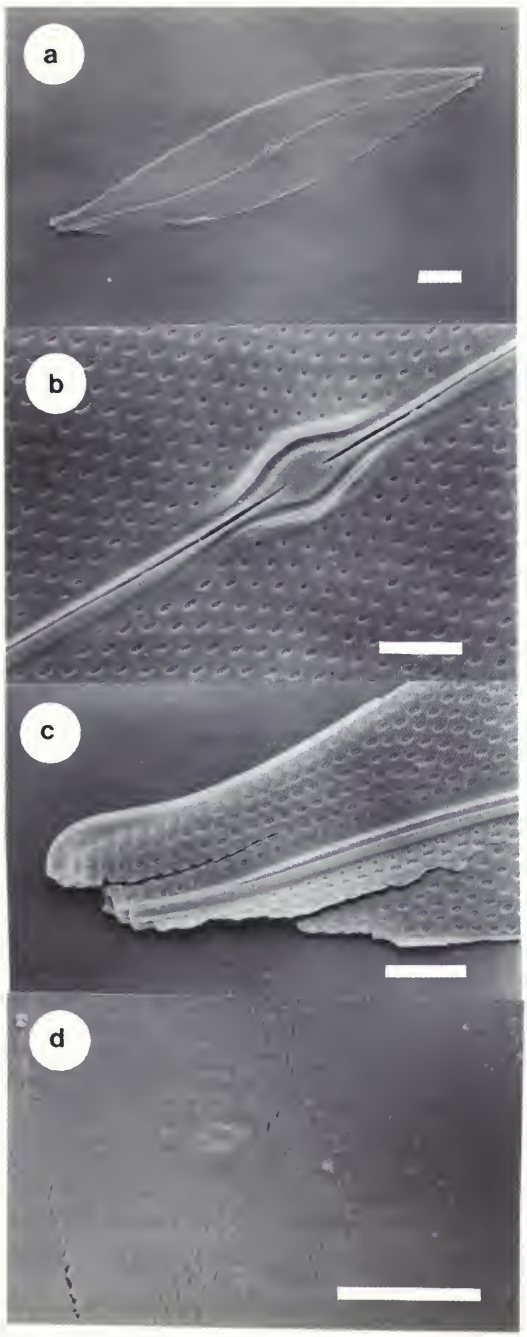

Fig. 4 *Pleurosigma aestuarii* (a) SEM of valve; (b) SEM of internal central area; (c) SEM of internal valve apex, showing change in striae orientation; (d) SEM of external central area. Material from letter of de Brébisson 27 February 1849 to Walker Arnott. (Scale bars: a = 10 µm; b, c = 2 µm; d = 5µm).

3. ***Pleurosigma aestuarii*** (Bréb.) W. Sm. in *A Synopsis of the British Diatomaceae*. **1**: 65, pl. 31 fig. 275 (1853). Type: France, St Vaast, n.d., *de Brébisson* s.n., BM100839!
Fig. 4

Navicula aestuarii Bréb. in Kützing, *Species Algarum*: 890 (1849).
Gyrosigma aestuarii (Bréb.) Griffith et Henfrey in *The Micrographic Dictionary*: 302, pl. 11 fig. 35 (1856).

Valves lanceolate, slightly sigmoid, apices rostrate (Fig. 4a). Length 60–90 µm, breadth 12–20 µm. Raphe central becoming eccentric towards the apices, strongly sigmoid. Internal central bars smooth and of equal length (Fig. 4b). Hyaline area absent from besides central bars (Fig. 4b). External central raphe fissures overlapping (Fig. 4d). Areolae not divided by a silica bar (Fig. 4b). Striae change orientation at the apex (Fig. 4c). Transverse and oblique striae 18 per 10 µm intersecting at 60°.

MATERIAL EXAMINED

FRANCE. St Vaast: n.d., *Kützing* 1567 (BM 18866); n.d., *Kützing* 1729 (BM 18867); n.d., *de Brébisson* s.n., (BM 100839); n.d., *de Brébisson* s.n., (BM 100840).

4. ***Pleurosigma mamoranqi* G. Reid *sp. nov.*** Type: New Zealand, South Island, Mamoranqi Bay, n.d., *S.R. Stidolph* s.n., BM81613!
Fig. 5

Valva rhombicus, sigmoideo, 100–120 µm longa, 15–19 µm lata. Raphe valde sigmoidea. Striae transapicales 26 per 10 µm, striae obliquae 16 per 10 µm. Poris habens transtrum. Transtra centralia laeves, in longitudine aequales, ovalis area hyalina.

Valves rhomboidal, sigmoid, length 100–120 µm, breadth 15–19 µm (Fig. 5a, h). Raphe strongly sigmoid and eccentric towards the apices (Fig. 5a, h). Areolae with a bar across them (Fig. 5c, e), transverse striae 26 per 10 µm, oblique striae 16 per 10 µm, intersecting at an angle of 56°, striae do not change orientation at the apex (Fig. 5 d–g). Internal areolae of a different shape around the helictoglossa (Fig. 5e). External central raphe fissures overlapping (Fig. 5b, g). Internal central bars smooth, approximately equal in length (Fig. 5c). Hyaline area adjacent to the central bars oval (Fig. 5c).

MATERIAL EXAMINED

NEW ZEALAND. South Island. Mamoranqi Bay, n.d., *S.R. Stidolph*, BM81613.

5. ***Pleurosigma lysekilii* G. Reid *sp. nov.*** Type: Sweden, Lysekil, n.d., *P.T. Cleve* s.n., BM12896! (Cleve & Möller no. 142; Deby collection).
Fig. 6

Pleurosigma angulatum f. *minor* Cleve in Cleve and Möller, *Diatoms (exsiccata)* **III**: 4, no. 142 (1878) nom. nud.

Valva lanceolatus ambitu ita leviter sigmoideo. Raphe centralis leviter sigmoidea. 160–262 µm longa, 20–30 µm lata. Striae transapicales 17–19 per 10 µm, striae obliquae 18–20 per 10 µm.

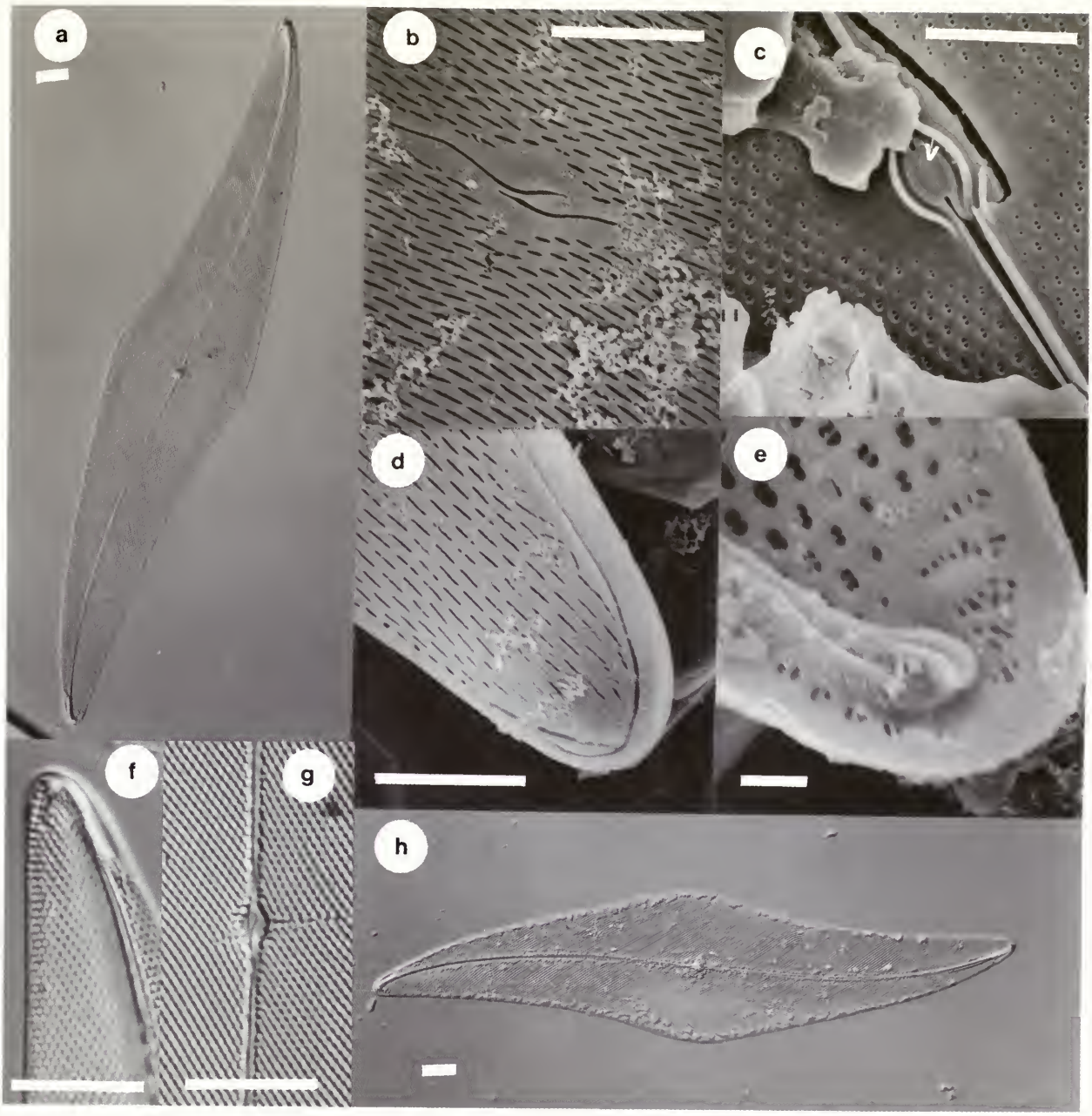

Fig. 5 ***Pleurosigma mamoranqi***. (a) BM 81613; (b) SEM of external central area; (c) SEM internal central area, arrow indicating extra siliceous deposit in middle of central nodule; (d) SEM of external valve apex; (e) SEM of internal valve apex; (f) light micrograph of valve apex (BM 81613); (g) light micrograph of central area showing external central raphe fissures (BM 81613); (h) BM 81613. SEM micrographs from New Zealand, Momoranqi Bay, ex *Stidolph* 155. (Scale bars: a, f–h = 10 μm; b, c = 5 μm; e = 1μm).

Valves lanceolate, only slightly sigmoid at the apices, subacute (Fig. 6a). Raphe central sigmoid at the apices (Fig. 6a). Length 160–262 μm, breadth 20–30 μm. Transverse striae 17–19 per 10 μm, oblique striae 18–20 per 10 μm, crossing at 58–61°. No change in the orientation of the striae at the apex (Fig. 6b) in contrast to *P. angulatum*. Central area small (Fig. 6b).

The name *Pleurosigma angulatum* f. *minor* Cleve and Möller cannot be applied to this taxon as it has prior use, *Pleurosigma angulatum* f. *minor* Rabenh. (1864). The taxon is not a form of *angulatum* in that it does not possess striae that change orientation at the apex.

MATERIAL EXAMINED

SWEDEN. Lysekil, n.d., *P.T. Cleve* s.n., Cleve & Möller no.142, Deby Coll., (BM 12896); 'W.Göteborg, Bahus', n.d., *P.T. Cleve* s.n., Cleve & Möller no.142, Wynne Baxter Coll.5342 (BM 59695).

6. ***Pleurosigma malmoensis* G. Reid *nom. nov.*** Type: Sweden, Malmö, n.d., *M.O. Nordstedt* s.n., BM 12902! (Cleve & Möller no. 136, Deby Collection).

Fig. 7

Pleurosigma aestuarii var. *minutum* Grunow in Cleve and Möller *Diatoms (exsiccata)* **III**: 3, no 136 (1878).

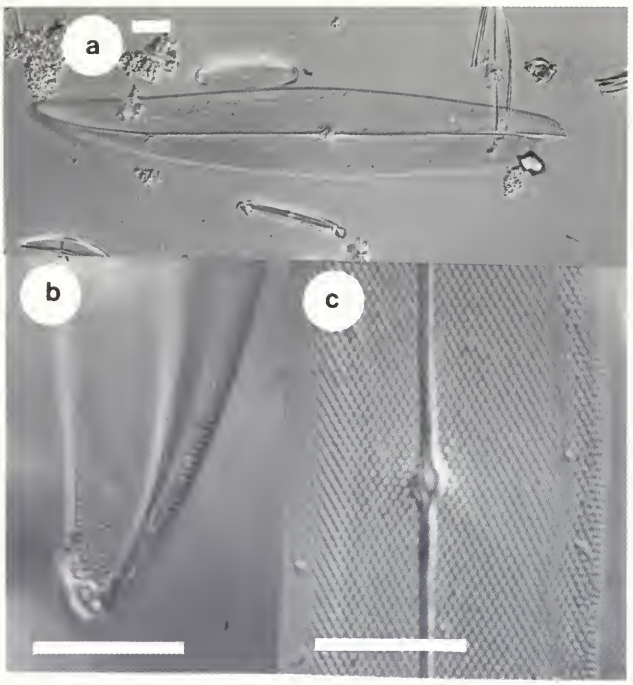

Fig. 6 ***Pleurosigma lysekilii.*** (a) BM 12896; (b) valve apex; (c) central area. (Scale bars: a–c = 10 µm).

Fig. 7 ***Pleurosigma malmoensis*** BM 12902. (Scale bars: a–b = 10 µm).

Pleurosigma minutum (Grunow) Cleve, *Kong. Sven. Vet. Hand.* **26**: 41 (1894).

Pleurosigma angulatum f. *minutum* (Grunow) De Toni, *Syll. Alg.*: 232 (1891).

Pleurosigma angulatum var. *minutum* (Grunow) McCall, *J. Linn. Soc. Lon. Bot.* **49(328):** 266 (1933).

Valves sigmoid, lanceolate, length 50–75 µm, breadth 12–15 µm (Fig. 7). Raphe central, sigmoid (Fig. 7). Transverse striae 26–27 per 10µm, oblique striae 28–29 per 10 µm, crossing at an angle of 60°. Central area small with smooth central bars of approximately equal length, there is no hyaline area adjacent to the central bars. External central fissures curved in the same directions (Fig. 7a). Striae do not change orientation at the apex (Fig. 7).

MATERIAL EXAMINED

SWEDEN. Malmö: n.d., *M.O. Nordstedt* s.n., Cleve & Möller. no. 136, Deby Coll. (BM 12902); n.d., *M.O. Nordstedt* s.n., Cleve & Möller no. 136 (BM – Adams Coll.).

7. ***Pleurosigma stidolphii*** Sterrenburg, *Bot. Mar.* **34:** 568, figs 38–46 (1991). Type: New Zealand, Otago Harbour, October 1961, *A.J. Doig* s.n., BM81608!

Fig. 8

Valves very rhombic, sigmoid, tapering to acute apices. 100–270 µm long; 30–60 µm wide (Fig. 8a). Valve vaulted with raphe situated on a ridge (Fig. 8a). Internal central bars with siliceous lateral extensions. Central area small (Fig. 8c). Oblique striae 22–25 per 10 µm;

Fig. 8 ***Pleurosigma stidolphii*** BM 81608. (Scale bars: a–c = 10 µm).

transverse striae 23–27 per 10 µm. Striae do not change orientation at the apex (Fig. 8b). Areolae undivided. External central raphe fissures overlapping.

MATERIAL EXAMINED

NEW ZEALAND. Otago Harbour, October 1961, *A.J. Doig* s.n., leg. S.R. Stidolph (BM 81608).

ACKNOWLEDGMENTS. I would like to thank Dave Williams and Eileen Cox for their help and comments on the paper and Peter York and Nick Hayes for help with photomicroscopy.

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